University of Alberta

Dynamics of Ungulate - Plant Grazing Systems

by

Moses Makonjio Okello

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

In

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Dynamics of Ungulate - Plant Grazing Systems** submitted by Moses Makonjio Okello in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Wildlife Ecology and Management.

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DEDICATION

This work is dedicated to the Lord who has seen my tears of loneliness and those of my wife Rose and daughter Irene. Thank you for your love and faithfulness.

To my father's household, all my teachers and friends who supported me in my graduate studies in North America. I will cherish the wonderful memories we share.

ABSTRACT

Grazing stability is determined by three main factors: (i) plant response to grazing, (ii) functional response (intake rate) of herbivores, and (iii) numerical response (population) of herbivores. This stability is investigated with 'predator-prey' graphs or simulation models. This thesis applies the 'predator-prey' approach to wapiti *(Cervus elaphus nelsoni)* grazing *Poa/Bromus* grassland openings in boreal mixedwood forests of central Alberta.

Forage dynamics of ungrazed and continuously grazed (irrigated, unirrigated and manured) pastures were determined by clipping and weighing green, dry and litter pools. Manured pasture had the highest green biomass (g/m^2) (261.1 ± 25.5, $r = 0.47$, $K = 227$, where r is rate of increase and K is maximum green biomass), followed in order by irrigated (197.7 ± 6.2, $r = 0.48$, $K = 198$), unirrigated (164.8 ± 6.9, $r = 0.69$, $K = 161$) and protected (123.5 ± 6.7, $r = 0.85$, $K = 123$). The response of forage to defoliation was determined using clipped plots. Forage compensated for defoliation if moderate and early in the growing season, otherwise cumulative productivity declined. Using movable cages on moderately stocked pasture, defoliation by wapiti was similar to hand-clipping in its impact on forage production. Daily forage removal by wapiti averaged 7.0 ± 0.6 kg/head/day. Removal depended on available biomass and grazing pressure. On winter pasture, snow cover influenced the efficiency of feeding but interactions between snow characteristics and forage biomass were

complex.

Experiments with habituated wapiti grazing hand - constructed swards provided details of the functional response. Intake rate, bite size and cropping rate depended on sward type (forbs, lush green, lawn or senescent). Bite size increased with fiber content and plant height. Cropping rate increased with protein and moisture content, but declined with bite size, plant height and fiber content. Intake rate (g/min) ranged from 21.48 ± 1.33 to 35.46 ± 1.99. Bite size (g/bite) ranged from 0.59 ± 0.03 to 1.34 ± 0.04. Cropping rate (bites/min) ranged from 15.90 ± 0.73 to 41.08 ± 1.55.

'Predator-prey' graphs predicted that the grazing system to be relatively stable with a single stable point at most stocking densities. However, enrichment through irrigation and nutrient enrichment appeared to have a destabilizing influence. This may have implications for prescribed burning and other range management programs in Elk Island National Park.

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CHAPTER 1
INTRODUCTION

PLANT - HERBIVORE INTERACTIONS

Ungulates introduced into a previously unoccupied habitat, often go through a series of population oscillations as they adjust to the forage supply (Caughley 1976a, 1976b). Oscillations usually dampen towards an equilibrium or may lock in a stable limit cycle. Less commonly, they crash (such as the spiral dive of reindeer on St. Matthew Island in the Bering Sea, Klein 1968). Vegetation follows a reciprocal trajectory, offset by about a quarter wavelength (Fig 1.1). This adjustment accompanies changes in vegetation composition, structure and productivity (Caughley 1977, Noy-Meir 1975).

These dynamics and the general stability of grazing ecosystems (in the absence of predation) are determined by three relationships (Fig. 1.2): 1) plant growth (production response), 2) grazing efficiency of herbivores (functional response) and 3) increase of animals in relation to plant availability (numerical response).

EQUILIBRIA AND TURNING POINTS

There are two ways to investigate stability in plant-herbivore interactions. One is to apply predator - prey graphs to set-stocked systems (Noy-Meir 1975). If the numerical response of the herbivore is known, further insights can be gained from plant herbivore - interactive models (Caughley 1976a).

Predator - prey graphs

General stability properties of simple fixed-stocked systems can be explored by graphical techniques (Fig. 1.3) supplemented by mathematical analysis of behavior near equilibrium points (Holling 1959, May 1973). However, few applications to real ecological data have been attempted (Noy-Meir 1975). One notable exception is Gaare and Skogland (1980) who studied lichen - reindeer interactions.

Herbivory is a special case of "predator-prey" interaction. Even though

much of the theory of trophic interactions comes from predator - prey interactions, and particularly for two animal populations, the herbivore ("predator") - plant ("prey") interaction is similar in its general features. Useful insights include investigating stability conditions for a specific grazing system (a given animal and vegetation) at a constant stocking rate and how stability changes with stocking rate.

Two graphs are needed: (i) growth response of plants, and (ii) functional response of the herbivore, both in relation to current plant biomass. These graphs are then superimposed and interpreted as in Noy-Meir (1975). The growth curve of plants is described:

$$G = g\,V\,(1 - V/K)$$

where G is change in forage biomass (primary productivity), g is instantaneous initial growth rate, V is vegetation biomass (per unit area) and K is the maximum grazable vegetation (carrying capacity). The curve generally is convex (G-curves in Fig 1.4) with a single maximum. The increase in the low biomass range expresses the increase in photosynthetic capacity with increasing leaf area. The plateau and the decline in higher biomass range expresses self-interference (shading, competition). At K, maintenance losses equal photosynthesis and G = 0 (Noy-Meir 1975).

The functional response is expressed as the daily rate of consumption of vegetation by a herbivore per unit area, c. This relationship has the shape of a saturation curve when consumption is plotted against some measure of vegetation. Consumption increases at low V and reaches a plateau at high V. At low V, intake is limited by forage availability and increases with it while, at high V, a saturation of intake capacity (digestion rate) is reached. One form of this relationship is the Michaelis-Menton equation (Wilmshurst et al. 1995):

$$c = c_{max}\,V / (V + K)$$

This relationship has also been expressed as a first-order differential equation (Caughley and Sinclair 1994): Intake = c (1 - Exp (-b V), where c is a constant, b is a slope of the curve that indicates grazing efficiency of a herbivore. Other versions of these models of functional response have been discussed by Shipley and Spalinger (1992) and Spalinger and Hobbs (1992). The slope (as in

Fig. 1.2b) expresses the "grazing efficiency" i.e. the extent to which a herbivore can find food to meet its requirements at low food densities.

Plant - herbivore interactive models

The components of this system are interactive: plant growth is determined by the accumulated biomass of vegetation, and indirectly by the density of animals eating them (Caughley 1976a, 1976b, 1977). In interactive models, plant and animal populations have their own dynamics, each affected by the other (Caughley 1976a).

Growth of ungrazed plants follows the logistic model. In the absence of herbivores, the vegetation increases from low density at its intrinsic rate of increase, a_1 . Sunlight, minerals and water are shared between the plants and therefore the initial rate of increase is slowed as biomass increases (due to competition for resources). This is approximated by the logistic term (1 - V / K), where V is the biomass of vegetation and K is the maximum sustainable biomass under the climatic and edaphic conditions. Hence, the exponential nature of growth takes the logistic form:

$$dV/dt = a_1 V (1 - V/K)$$

In the presence of herbivores, net biomass accumulation is slowed or reversed by grazing. With allowances for trampling, the removal rate is equal to the product of the animals, N, and the average rate of consumption of each animal, c_1. As V declines, the amount of vegetation eaten by each herbivore also declines. This "functional response" describes a decline in consumption rate as the biomass of resource (food) increases, approaching unity at saturation. This is described by the Michaelis-Menton relationship ($V / V + V_{50}$), where V_{50} is the biomass at half the maximum rate of consumption (approximation to estimate the effect of this saturation). Another approximation is Ivlev's term, $1 - e^{-d1V}$ (Holling 1959) where d_1 is the rate at which satiation is approached with increase in V . This modifies the logistic equation:

$$dV/dt = a_1 V (1 - V / K) - c_1 N [V / (V + V_{50})]$$

Herbivore numbers decline at a constant maximum rate per head, a2, in the absence of vegetation (due to starvation). When the vegetation is abundant so that the animals eat as much as they desire, this rate of decline is ameliorated

by a constant rate, c2. Therefore, the rate of increase can be represented as c2 - a2. At intermediate levels of vegetation density (biomass), the degree to which the maximum rate of decrease is compensated for by food supply is approximated by multiplying c2 with a saturation term. This term is often equivalent to that of functional response because the rate of herbivore population increase is equivalent to the rate at which satiation is achieved (their foraging efficiency). This so-called "numerical response" (Caughley 1976a) can be expressed:

$$dN/dt = N [- a_2 + c_2 (V / V+ V_{50})]$$

For such a system, the equilibrium for plants is determined by animal attributes (rate of increase of animal numbers with abundant food, rate of maximum decline with an absence of food and efficiency of foraging of herbivores). However, the equilibrium for herbivores is determined by vegetation biomass, their rate of consumption and foraging efficiency (Noy-Meir 1975, Caughley 1976a).

If the vegetation intrinsic rate of increase is modified or the maximum density of vegetation biomass in the absence of grazing is modified, the equilibrium level of vegetation will be unaffected because there will be a corresponding increase in herbivore numbers. Herbivores which are efficient in finding and utilizing food will die out rapidly if they tend to hold the vegetation below half it's ungrazed equilibrium biomass (May 1973, Caughley 1976a).

The interactive system of vegetation and herbivores represented in the models discussed define equilibrium points (V* for plants, and N* for herbivores) as:

$$V^* = 1 / d_2 \log_e [(c_2 / (c_2 - a_2)],$$

$$N^* = [V^* a_1 (1 - V^*/ K)] \ / \ \{c1[V / (V + V_{50})]\}$$

$$\text{where } d_2 = (1 / V) \log_e [V_{50}/ (V + V_{50})]$$

Population growth will be determined by the efficiency with which herbivores utilize plants, the efficiency of animals converting plants into new animal numbers, the rate of increase of animals and forage consumption rate. Equilibrium is bound by the points:

$$d_1 V^* > 5 \text{ and } K > 2 V^*$$

where d_1 is the efficiency of the functional response.

PLANT - HERBIVORE EQUILIBRIUM AND CARRYING CAPACITY

A herbivore - plant equilibrium where the rate of sustained forage production by plants equals the rate of forage consumption of plants by herbivores, without human influence, is at "ecological carrying capacity". At that equilibrium, birth rate equals death rate, and body condition and health of herbivores is often poor. This equilibrium is what wildlife managers (especially in parks) call "ecological carrying capacity" and is normally attainable without human influence (Caughley 1977). "Economic carrying capacity" is a plant - herbivore equilibrium that yields maximum sustained yield and is enforced by specific removals (hunting or trapping). This is the carrying capacity relevant to livestock owners and game ranchers.

The natural (unmanaged) equilibrium between plants and herbivores can be called "ecological carrying capacity" (Fig. 1.3) whereas a target equilibrium for sustainable utilization goals, or habitat management goals, result in "carrying capacity" at any point along a zero - isocline of vegetation. The zero - isocline describes a range of other equilibrium points between plants and herbivores depending on management goals. This range of plant - herbivore equilibria maintained by specific off-takes is always lower than "ecological carrying capacity" (Caughley 1977).

Although plants and animals may stabilize following perturbations or eruptions (Caughley 1976a), some grazing systems may be so fragmented and natural controls so modified that they are incapable of stabilizing the relationship. Further, we do not know the critical ecosystem size at which a stable equilibrium is possible. Carrying capacity of such compromised systems must be considered in terms of target plant-herbivore population size rather than equilibrium populations. The factors which principally regulate herbivore populations are depletion of food, animal dispersal and predation. Where dispersal is nonexistent and predation is insignificant, forage becomes the major variable affecting herbivore body condition and population size.

Carrying capacity for wild ruminants is often calculated on the basis of allowable forage removals, which ensure long term maintenance of range

productivity without consideration whether an animal can meet its food requirements (Mentis and Duke 1976, Hudson and Watkins 1986, Hanley and Rogers 1989). Quality, composition and structure of forage may be more significant in determining carrying capacity than quantity. Limit of daily food intake is determined by rumen capacity (forage quality) and the logistics of feeding (forage availability).

PROBLEM AND JUSTIFICATION

When ecosystems are fragmented or surrounded by intensive human activities (farming, urbanization or constructions of roads and other structures), natural migration and distribution patterns established over long periods of time by herbivores are disrupted. Many conservation areas are faced by these problems as human population and other activities crowd conservation areas (such as national parks). Elk Island National Park in central Alberta has been affected by such "insularizing" factors.

Elk Island National Park, located 30 km east of Edmonton in central Alberta, has been actively managed to regulate ungulate populations. This is changing, as active management has been restrained to allow ungulates to achieve an equilibrium with forage supply (Blyth and Hudson 1987, Blyth 1995). This thesis investigates equilibria and turning points of one ungulate (wapiti, *Cervus elaphus nelsoni*) in a boreal mixedwood forest ecosystem within which the park lies.

This information supplements a program of studies (Blyth and Hudson 1987, Cool 1992) on herbivore populations, forage dynamics and interactions. In a recent thesis, Blyth (1995) explored the numerical response of ungulate populations using time - series analysis. This work complements current modeling efforts of the ungulate - grazing system at Elk Island National Park.

OBJECTIVES

Specific objectives were to:

- determine plant biomass accumulation over the growing season, and explore factors that determine the dynamics of pasture growth,
- determine forage intake rates of wapiti in winter and summer, the

pattern of intake rates with forage biomass, and factors that affect this response,

- use these relationships to investigate stability of wapiti - forage grazing system using predator - prey graphs.

The findings along with those of a companion study (Blyth 1995) are applied to understanding the stability of grazing systems and the consequences of management actions in Elk Island National Park.

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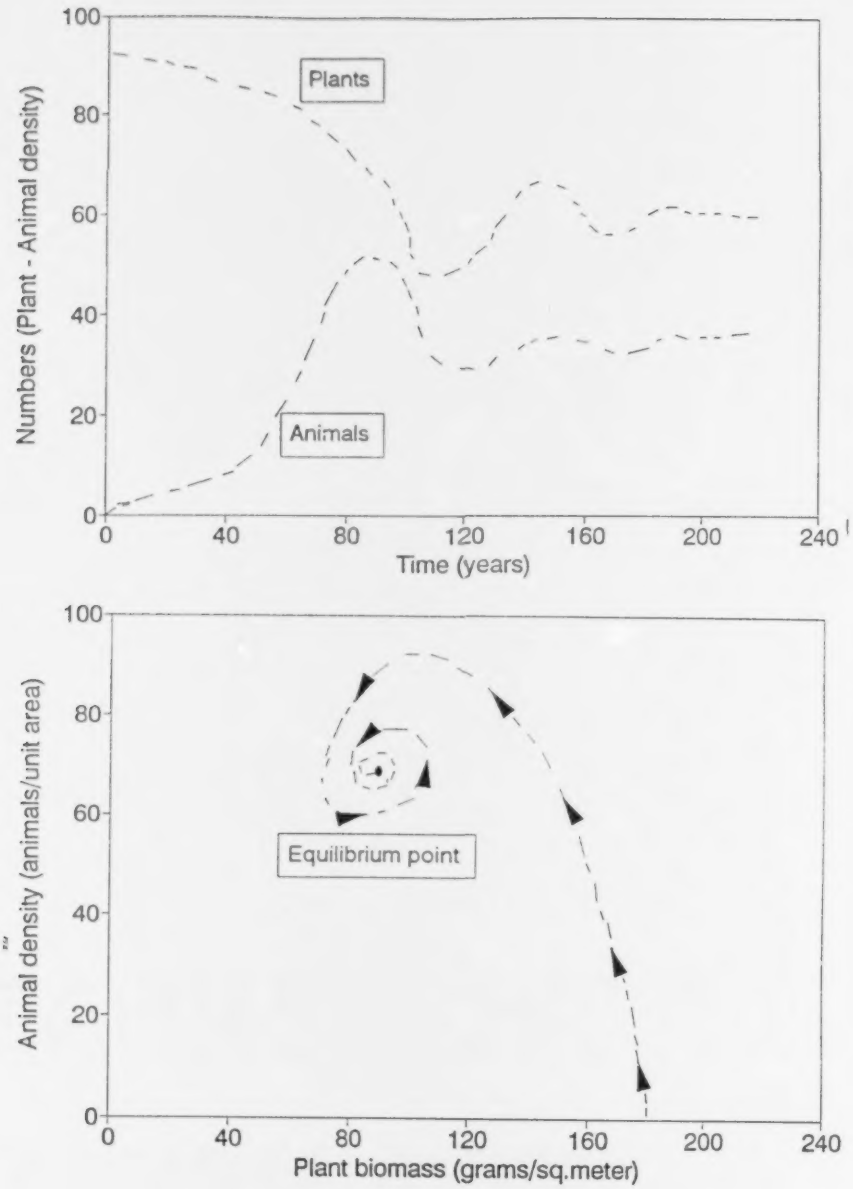

Fig. 1.1. The trajectory of plants and animals during an ungulate eruption. Animal density increases initially, then fluctuates and stabilizes with plant biomass (top). Plant biomass declines initially then fluctuates until it stabilizes at an equilibrium point with herbivore density (bottom).

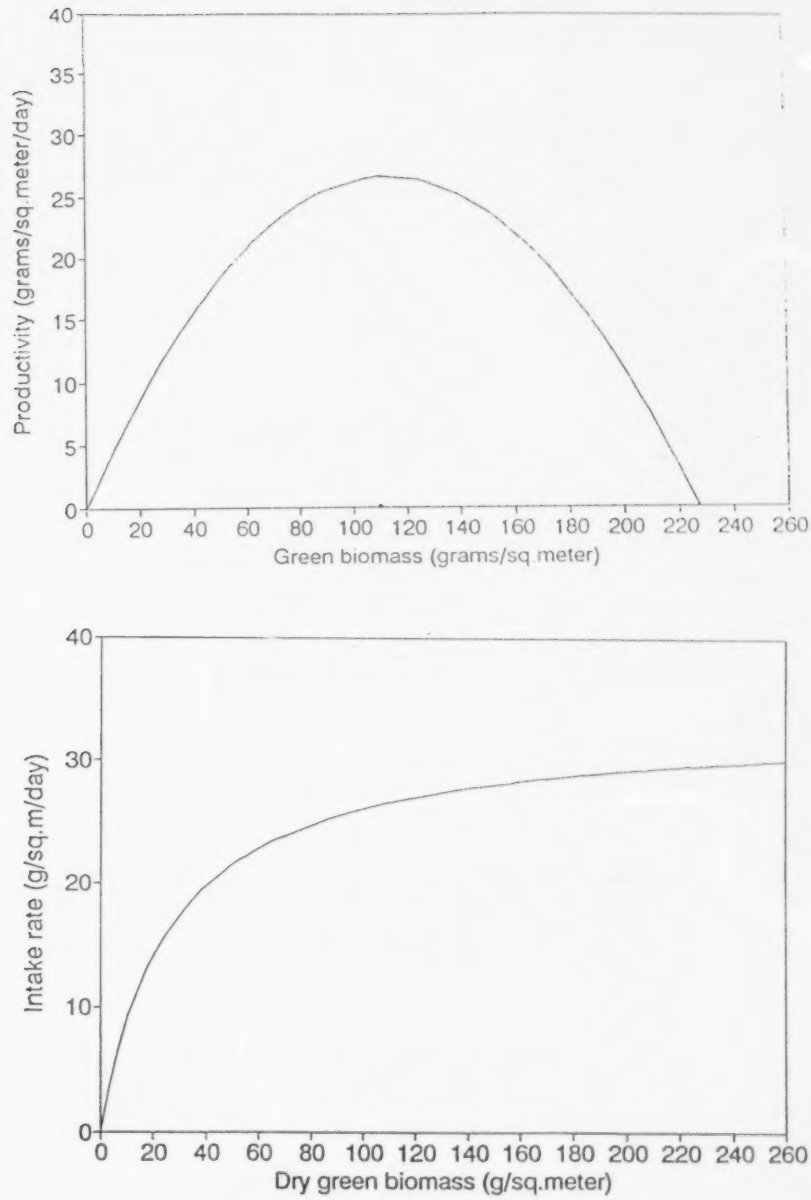

Fig. 1. 2. Dynamic components of a plant - herbivore system. The growth response (plant growth curves) of plants (top), and the change in forage intake rate (functional response) with biomass or its attribute like bite size (bottom). Change in herbivore numbers with bite size or attribute of biomass (numerical response) is similar in shape to the functional response.

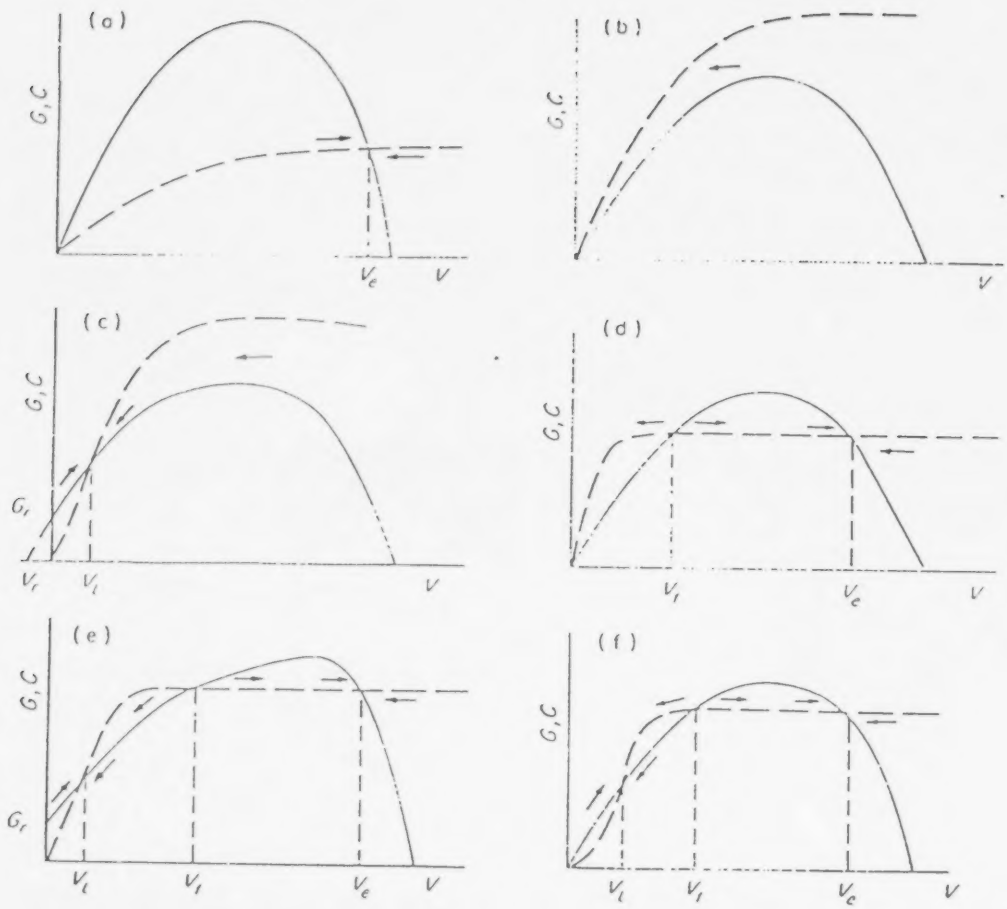

Fig. 1.3. Possible stability combinations of G-(vegetation growth) and C-(herbivore consumption) curves at a given herbivore density , H. (a) Undergrazed stable steady - state (Ve). (b) Overgrazed to extinction. (c) Overgrazed to a low biomass steady - state (Vl); Vr - reserve (ungrazed) biomass, Gr - residual growth potential. (d) Steady - state and unstable turning point (Vt) to extinction. (e) Two steady - states (Ve, Vl) separated by turning point (f) as (e), but caused by sigmoid C - curve, not by ungrazable plant reserve. (After Noy - Meir 1975).

CHAPTER 2
DYNAMICS OF PASTURE PRODUCTION

INTRODUCTION

Plant production is an important component in the stability of grazing systems (Chapter 1). In the absence of herbivores, vegetation (V) increases from low density at its intrinsic rate of increase, a_1 . Sunlight, minerals and water are shared by plants (Harper 1977, Krebs 1985, Begon and Mortimer 1986) and therefore the initial rate of increase is slowed as biomass increases due to competition for resources. This effect is approximated by the logistic term (1 - V / K), where V is the biomass of vegetation and K is the maximum sustainable biomass under prevailing climatic and edaphic conditions (Krebs 1985, Mortimer and Begon 1986). Hence, the exponential nature of growth is modified into the logistic form:

$$dV/dt = a1\ V\ (1 - V / K)$$

Plant (rather than herbivore) populations follow this logistic pattern as plants best satisfy the assumptions of the model, that the limiting resources available for plant growth and reproduction (moisture, nutrients and light) are inert, have a constant rate of renewal influenced only by availability (Harper 1977, McNaughton 1979, Krebs 1985).

Two hypotheses were tested; namely, that forage biomass accumulation on ungrazed areas follows the logistic pattern, and that moisture (irrigation), nutrients (manure) and grazing determine both the maximum biomass (carrying capacity) and rate of forage production. Specifically, I attempted to:

- determine the pattern of plant biomass accumulation (green, dry and litter pools) over the growing season,
- determine the effect on biomass accumulation of grazing, moisture (irrigation) and manuring,
- estimate the rate of increase (r), maximum green biomass (K) and forage biomass changes under different conditions (irrigated, manured, grazed).

METHODS

Study area

The study was conducted at the Ministik Wildlife Research Station, Alberta, Canada. The area is characterized by low hills with scattered lakes and ponds. Plant growth begins in late April and ends in October. Permanent snow cover is established in November and persists until April. The major vegetation types are *Populus* forest, *Bromus - Poa* grassland and *Carex* wetland. The grasses are dominated by bromegrass (*Bromus pumpellianus*) and Kentucky bluegrass (*Poa pratensis*). Dicotyledonous plants include dandelion (*Taraxacum officinale*), clovers (*Trifolium* spp.), *Achillea millefolium*, Aster (*Aster spp.*), Canadian thistle (*Cirsium arvense*) and wild strawberry (*Fragaria virginianus*). Except for several permanent exclosures, pastures used in this study were grazed by Rocky Mountain wapiti (*Cervus elaphus nelsoni*) stocked at approximately one animal/ha. The year of the study (1994) was comparable (in terms of rainfall) to other years.

Field pasture plots

Two pairs of exclosures (30 meters by 30 meters each) were established on previously grazed pasture. For each pair, one plot was irrigated (using a sprinkler) and the other was unirrigated. Irrigation was done in the evenings at least every two days except when it had rained heavily. The two pairs of exclosures were located about 50 meters from each other. In a separate pasture (about 0.5 km a way), one additional unirrigated pasture (same dimensions) was established. There was no treatment replication.

To evaluate nutrient enrichment, I selected "manured plots" with a high concentration of fecal pellets (and possibly urine deposits) from previous winter accumulation. Two (10 meters by 10 meters) "manured" plots were established in the same pasture and sampled in the same manner as ungrazed, irrigated and unirrigated plots.

To test the effect of long - term grazing on plant growth and composition, I also established protected plots on benchmark areas protected from grazing for over ten years. Two (40 meters by 40 meters each) plots were staked in these

permanent exclosures. The plots were about 0.5 km apart but in the same range type, soil and microclimate.

Sampling procedure

Sampling began in early May and ended in early October 1994. In each plot (ungrazed or protected, irrigated, unirrigated and manured), a quadrat of 30 cm by 30 cm was used to locate random areas to be clipped. To locate a random position, one corner of the plot was randomly selected (using random number generator on a calculator), and "a meter" interval picked randomly on the x- axis and y - axis grid. The quadrat was then placed at the edge of the intersection point on the x - y grid and forage inside the quadrat clipped.

Plants in each sample quadrat were clipped to the ground using shears, placed in labeled brown paper bags. Two samples were taken daily from each "treatment" after two to four days. Only means for any sampling day were used in subsequent analysis.

Samples were oven dried at 60 C for a minimum of five days. After drying, forage was separated into green, dry and litter, and weighed. Selected samples from each treatment were analyzed for protein using an FP-428 Automatic Nitrogen Determinator (1992 Leco Corporation®).

Data analysis and modeling

The instantaneous rate of increase (r) was calculated from green biomass data collected on consecutive sampling days. Data from a sampling day was divided by that of a previous sampling day to obtain a finite rate (finite rate of increase, λ). A natural logarithm of this finite rate estimated the instantaneous rate of increase, r. Only positive values of instantaneous rate of increase were used because they indicated a positive change in forage dynamics. A mean instantaneous rate of increase was estimated for each treatment (irrigated, unirrigated, protected and manured).

Instantaneous rate of increase and green biomass data were used to model productivity curves green biomass dynamics for each treatment. Instantaneous rate of increase and green biomass values were substituted in the integral form of logistic model (in non-linear iteration procedure) to estimate the

maximum green biomass, K. Calculated mean values for instantaneous rate of increase and estimates of K were used to model changes in plant productivity with biomass (for each treatment) using the differential form of logistic equation:

Green biomass = K / (1 + Exp (constant - (r * days)).

where K is maximum green biomass, r is the instantaneous rate of increase, and days are expressed as Julian day.

Data were categorized into spring, summer and fall seasons to find trends of green, dry (senescent) and litter. Spring began on 15 April (Julian day 104) to 3 June (Julian day 154). Summer began on 4 June (Julian day 155) to 31 July (Julian day 212). Fall began on 1 August (Julian day 213) and the remaining part of the study (end of September).

Seasonal data were analyzed as a repeated measures design. The general linear model (GLM) procedure of SAS was used with the raw data while Repeated Measure ANOVA was used on average values of each treatment (taking plots as replicates) for each season (repeated measure). Using general linear model procedure of SAS, the effect of treatments (protected, irrigated, unirrigated and manured) were tested using TREATMENT(PLOT) error term while the effect of season and the treatment*season interaction were tested using PLOT* SEASON (TREATMENT) error term. Repeated measures ANOVA used the same error term but considered seasons as repeated and used average values for each plot and season.

Simple correlations were done with the Pearson method, whereas multiple comparisons tests following significant tests were done with Tukey's Multiple Comparison method (Zar 1984). Non - linear model fitting and iterations, and computations were completed with SYSTAT® software (Wilkinson 1990). Significant difference was inferred at Type 1 error of less than 0.05.

RESULTS

Seasonal dynamics of green, dry and litter forage pools are compared in Figs 2.1-2.4.

Green biomass

Manured pasture (Fig. 2.1) had higher green biomass than protected (ungrazed) pasture ($P < 0.001$) and unirrigated pasture ($P = 0.005$). However, green biomass in manured and irrigated (Fig 2.1) pastures were not different ($P = 0.477$). Irrigated pasture had higher average green biomass than protected pasture ($P = 0.001$) but did not differ from unirrigated pasture ($P = 0.235$). Green biomass in unirrigated (control) pasture did not differ from protected pasture (Fig. 2.2). Protected (ungrazed) pasture had the highest average dry (senescent) plant material (123.1 ± 6.4 g/m^2), followed by manured pasture (26.4 ± 3.1 g/m^2).

Dry biomass

Dry biomass was greatest in unirrigated pasture (24.8 ± 3.4 g/m^2) and least in irrigated pasture (22.4 ± 4.0 g/m^2). Protected pasture had higher dry material than all pastures ($P < 0.001$ in all pairwise comparisons). However, manured pasture did not differ in dry material from irrigated pasture ($P = 0.93$) and unirrigated pasture ($P = 0.99$). Irrigated pasture did not differ in dry plant material from unirrigated pasture ($P = 0.98$).

Litter

Protected pasture contained the most litter (110.9 ± 7.0 g/m^2) followed by manured pasture (14.5 ± 2.1 g/m^2). Irrigated pasture followed with 13.4 ± 3.1 g/m^2, and lastly unirrigated pasture (13.1 ± 2.6 g/m^2). Protected pasture had higher litter than all pastures ($P < 0.001$ in all pairwise comparisons). However, litter content in manured pasture did not differ from irrigated pasture ($P = 0.998$) and unirrigated pasture ($P = 0.996$). Irrigated pasture did not differ in litter content from unirrigated pasture ($P = 0.748$).

Protected (ungrazed) pasture had a comparatively large proportion of dry (senescent) and litter material (Fig. 2.3). It seems that grazing removed most plant material that could turn into litter. Across all treatments, green biomass increased from spring, peaking in summer and slightly dropping in the fall as more plants became senescent. Dry material was highest in the fall and spring. Litter accumulation, however, was high in the fall and summer.

Instantaneous growth rate

Average instantaneous rates of increase were highest in protected (ungrazed) pasture (0.85 ± 0.13), followed by unirrigated pasture (0.69 ± 0.12), then irrigated pasture (0.48 ± 0.13) and lastly manured pasture (0.47 ± 0.11). Protected (ungrazed) pasture had higher instantaneous rate of growth than manured ($P < 0.001$) and irrigated ($P < 0.001$) pastures. Other pastures did not differ ($P > 0.7$ for all pairwise comparisons). Plots associated with a high average green biomass had a comparatively lower instantaneous rate of growth.

By substituting instantaneous rate of increase in the integrated logistic model and using non - linear iteration, the highest K was estimated for manured pasture (K = 227, constant = -113.57, $R^2 = 0.48$). Irrigated pasture had next high estimation of K (K = 198, constant = -32.29, $R^2 = 0.35$), followed by unirrigated pasture (K = 161, constant = -63.36, $R^2 = 0.58$), and lastly protected (ungrazed) pasture (K = 123, constant = -3.76, $R^2 = 0.44$). The instantaneous rate of growth and the estimated K values were substituted in the differential logistic model to model productivity changes with biomass (Fig 2.5).

Protein content

Protein content of plants declined with Julian day. Spring had the highest content (15.17 ± 0.64 %), followed by summer (12.90 ± 0.29 %) and lastly fall season (11.42 ± 0.88 %). These trends are expected as nutrients are depleted with increasing plant growth and biomass.

DISCUSSION

Manuring and irrigation increased pasture production. Manure provides plants with nutrients (especially nitrogen) and therefore relaxes constraints imposed by these. Irrigation supplies moisture for plant growth. However, the fact that irrigated pasture and unirrigated pasture did not significantly differ in average green biomass is an indication that moisture was not a dominant limiting factor during the study. However, this does not discount the importance of moisture as a limiting factor in other pastures or different years.

A mixed sward was considered for this work rather than single forage species. Therefore, deviation from the logistic pattern may be due to the

summation of individual logistic patterns. This deviation does not discount the general logistic pattern observed (Fig 2.1 and 2.2).

Green biomass also differed with the time of growing season. Plants begin to grow in early spring when conditions for growth are improving from winter dormancy. Most plants are adapted to rapid growth at this time so as to start photosynthesis and store energy needed for growth and new leaf production (Harper 1977). Many tillers sprout and overall production is enhanced to produce more leaves. Most plants try to put out new shoots as well as to produce the first inflorescence of the season. This explains why average green biomass increases throughout the growing season.

Green forage biomass increases to a summer peak which coincides with maximum leaf area and optimum growing conditions. Consequently, nutrients (e.g. protein) continue to decline. However, the rate of biomass accumulation declines at this time because of increased competition for resources (light, nutrients and space). This is the point when net primary productivity starts to decline due to competition among tillers. More plant leaves begin to senesce as reproductive tillers mature. As plants mature, products of photosynthesis are directed into production of seeds and fruits rather than new tillers.

Dry (senescent) material increases in the fall and then spring because most green plant material senesces in winter, but is gradually replaced in spring by new season growth. There is least senescence at peak growing season in late spring and summer. Dry plant material is not an important forage component in the growing season as there is abundant green forage and therefore forms a negligible proportion of forage. However, this changes in winter.

Senescent and litter material accumulates in protected (ungrazed) plots. Ungrazed forage composition is dominated by erect tall growing species. The thick layer of litter prevents more tillers from sprouting. Tall erect species (*Bromus* in this case) crowd short species. The low green biomass in ungrazed pasture can therefore be explained by the effect of a layer of litter preventing tillering, the tall *Bromus* structure that out - competes short plant species (such as forbs) and prevents light reaching the tillering meristems, and causes a high rate of senescence. Therefore, grazing may be "good" for adapted forage plants (McNaughton 1979, Owen-Smith 1988).

Grazing and fire have similar effects on rangeland productivity (Bailey 1988, 1993). Herbivory and fire reduce litter accumulation. Where ecosystems are regulated by fire, accumulation of litter (fuel) encourage fire which then consumes and recycles nutrients by oxidizing old plant materials. In many natural grazing ecosystems, pasture productivity can be maintained by both wild herbivores and fire (Sinclair and Norton-Griffiths 1979).

Plants with a high K seemed to have a comparatively lower instantaneous rate of growth. Possibly, plant communities with a lower K have few dominant plant species with reduced competition. Growth is therefore less limited by intraspecific and interspecific competition. A high K requires a longer time to achieve carrying capacity and therefore plants experience more intraspecific and interspecific competition. This limits growth and therefore accumulation of new plant carbohydrates and other nutrient accumulation though photosynthesis is comparatively slower (Begon and Mortimer 1986).

Because of the interaction between season and treatment, the effects of each should be interpreted with caution. An alternative experimental design (possibly a nested design) could provide a more reliable picture of the interactions of treatments and seasons. Nevertheless, the general effects of treatments and seasons confirms expectations.

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Table 2.1. Forage production, green biomass accumulation, dry (senescent) material, and litter across seasons for each treatment.

Pasture treatment [1]	Growing season	Green plant material (g/m^2) Mean ± S.E (n)	Dry plant material (g/m^2) Mean ± S.E (n)	Litter (g/m^2) Mean ± S.E (n)
Pasture with organic manure available	Spring	156.1±25.2 (11)	52.2±10.0 (11)	6.9±1.0 (11)
	Summer	274.8 ± 2.3 (15)	28.9± 3.3 (15)	10.8 ± 1.2 (15)
	Fall	251.9± 9.6 (2)	35.2 ± 6.6 (2)	15.0 ± 2.3 (2)
Pasture irrigated to provide unlimited moisture	Spring	130.2±12.7 (9)	41.6± 4.6 (9)	3.9±0.9 (9)
	Summer	230.2± 13.3 (15)	36.1± 2.6 (15)	10.1 ± 3.9 (15)
	Fall	217.6± 4.1 (6)	35.6± 5.7 (6)	15.6± 0.5 (6)
Plots protected from grazing for periods of over 10 years.	Spring	48.1±7.5 (13)	45.4±2.5 (13)	85.3±7.6 (13)
	Summer	173.9± 15.1 (15)	39.6 ± 6.1 (15)	130.6± 11.5 (15)
	Fall	160.6 ±17.9 (6)	43.8± 5.5 (6)	117.2± 10.2 (6)
Unirrigated (control) pasture. A most representative pasture of the area	Spring	59.2±12.0 (12)	27.9±3.2 (12)	5.73±1.0 (12)
	Summer	220.9± 13.5 (17)	17.5± 1.1 (17)	11.6± 3.7 (17)
	Fall	191.4± 16.1 (6)	31.6± 5.4 (6)	29.4± 8.5 (6)

[1]Spring (15 Apr-3 June), summer (4 Jun-31 Jul), and fall (1 Aug-30 Sep).

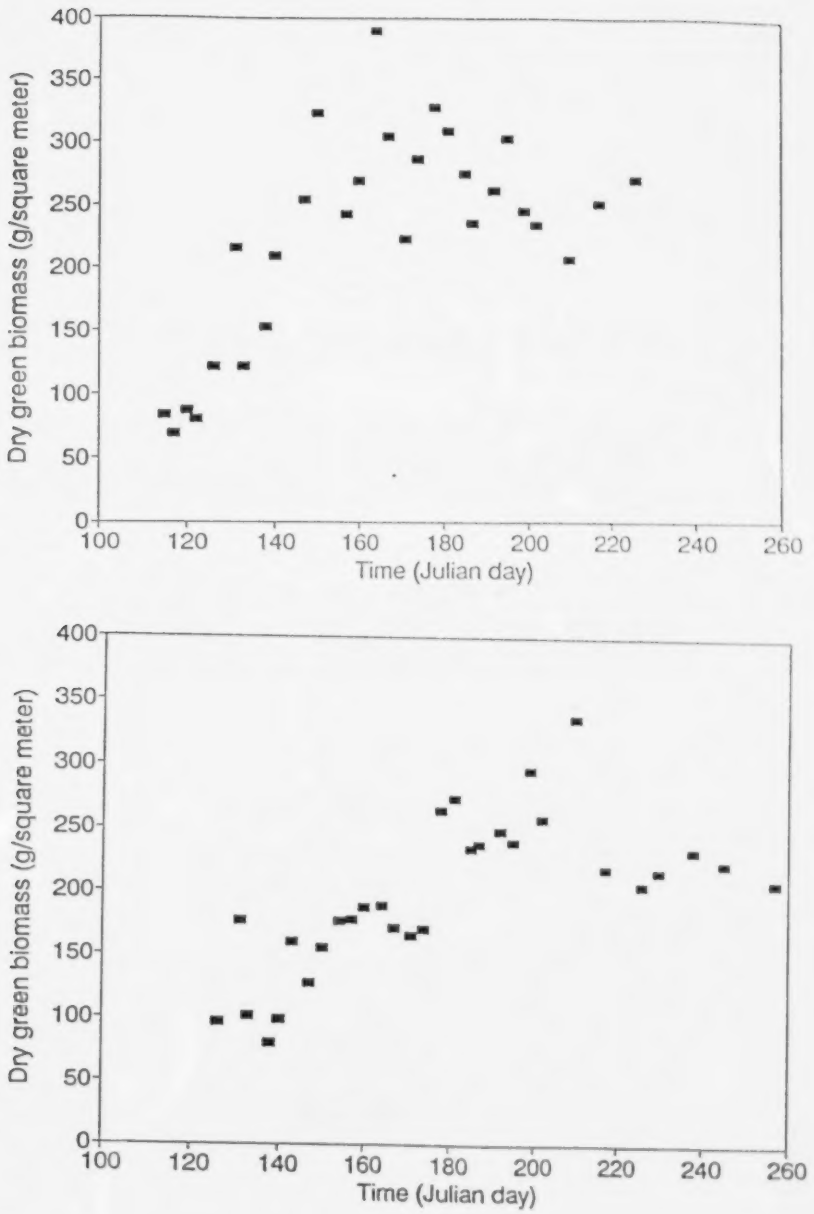

Fig. 2.1. Green biomass accumulation in manured (top), and irrigated (bottom) pastures. Biomass increased with time (Julian day), peaking and then beginning to decline as green biomass turned senescent.

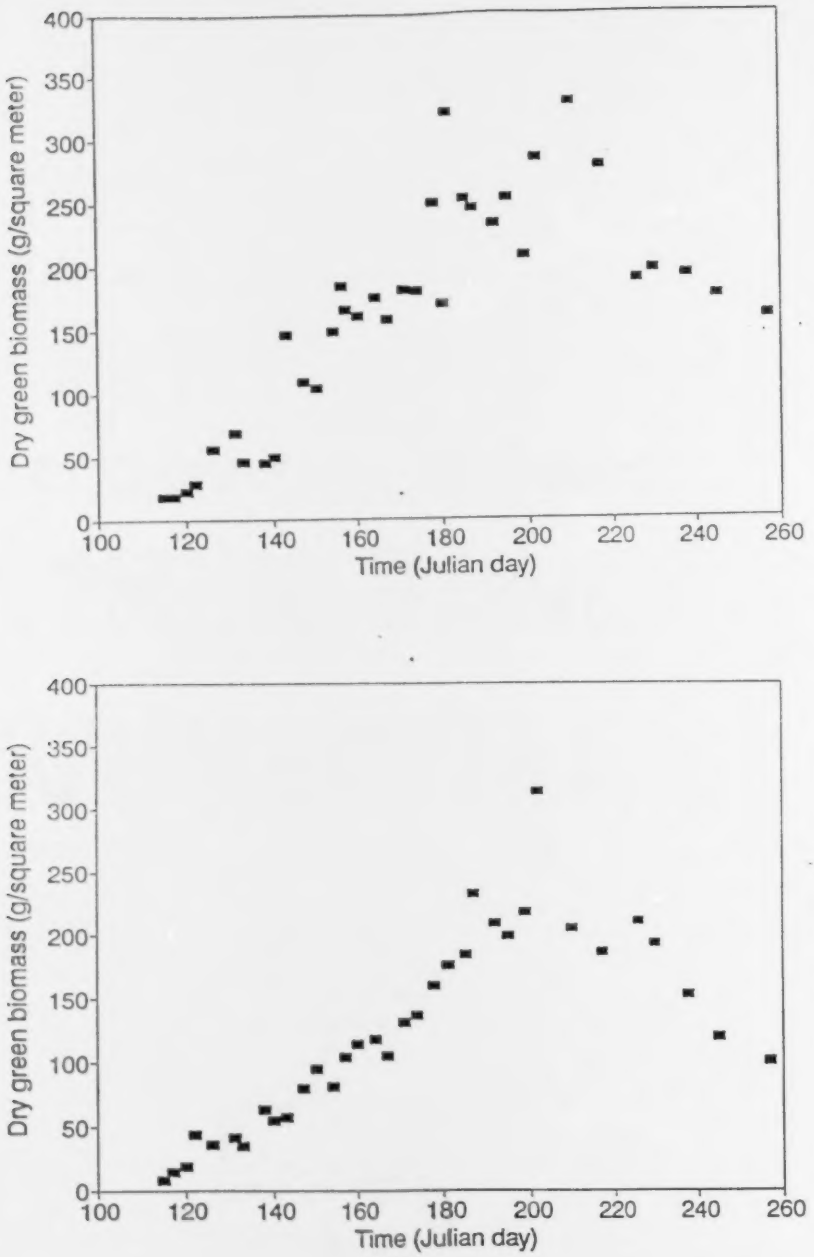

Fig. 2.2. Green biomass accumulation in unirrigated (top), and (ungrazed) protected (bottom) pastures.

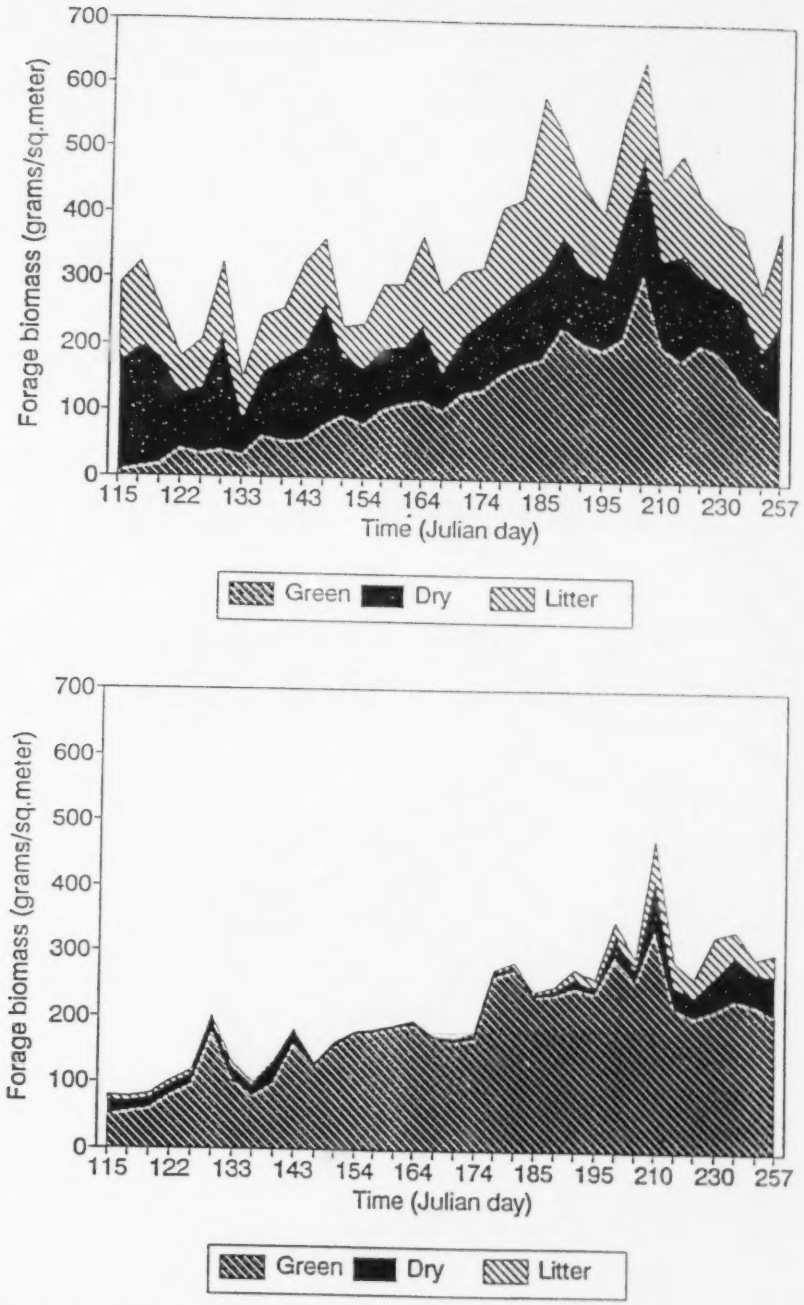

Fig. 2.3. Forage biomass by components (green, dry and litter) in protected (ungrazed) (top), and manured (bottom) pastures.

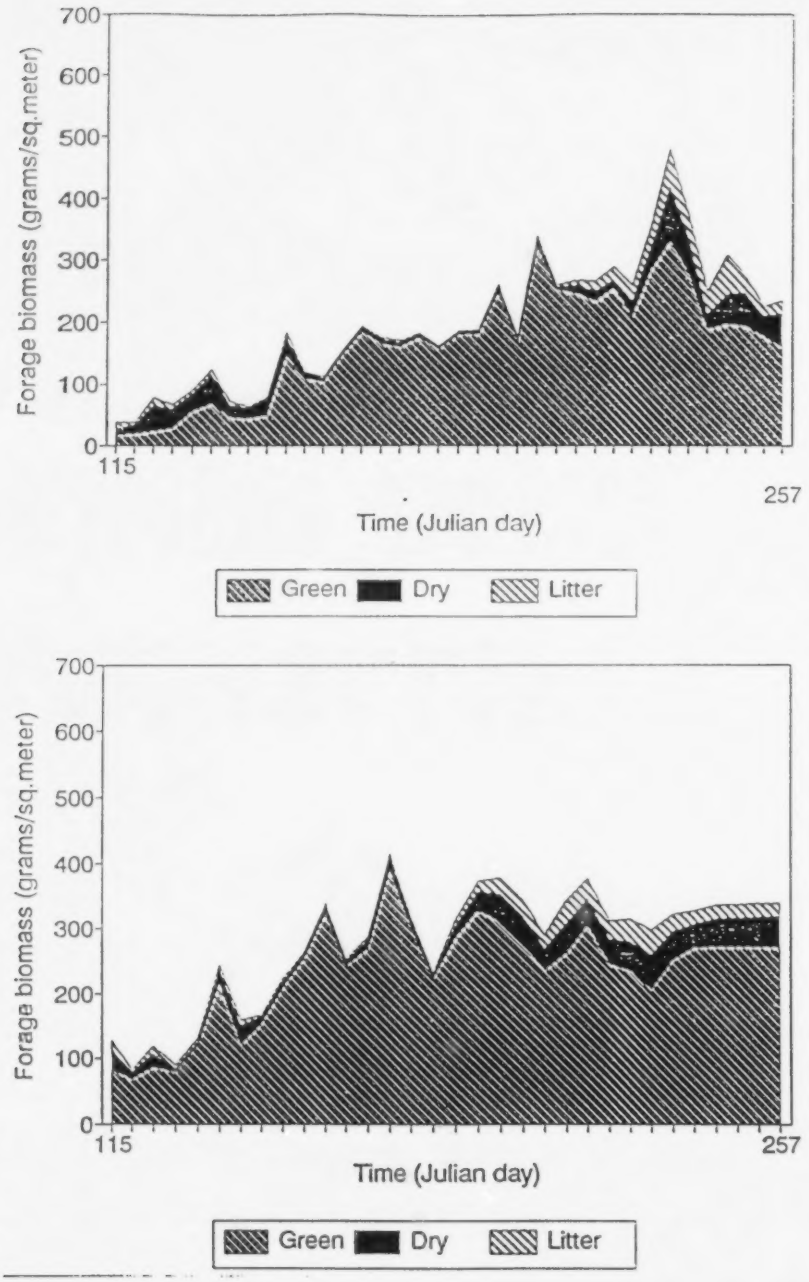

Fig. 2.4. Forage biomass by components (green, dry and litter) in unirrigated (top), and manured (bottom) pastures

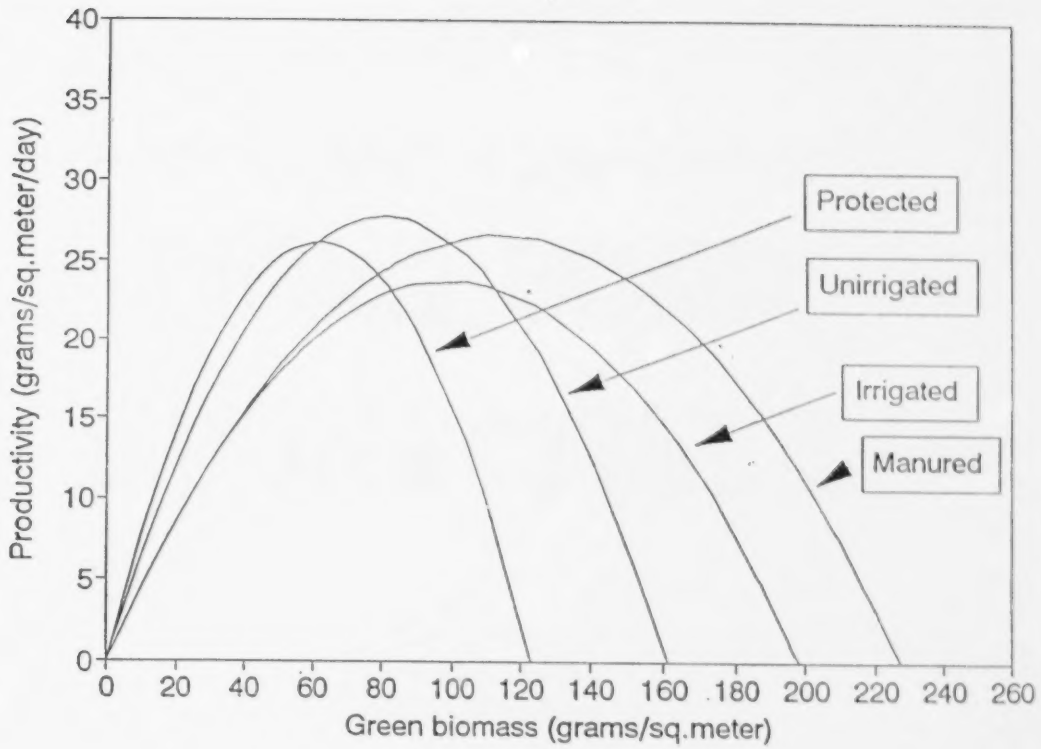

Fig. 2.5. The productivity pattern (g, $g/m^2/d$) with biomass (V, g/m^2) of four pasture treatments: (ungrazed) protected ($g = 0.85\ V(1 - V/123)$), irrigated ($g = 0.48\ V(1- V / 198)$), unirrigated ($g = 0.69\ V\ (1 - V /161)$), and manured ($g = 0.47\ V(1 - V / 227)$).

CHAPTER 3
PLANT RESPONSE TO CLIPPING

INTRODUCTION

Plant productivity (daily increment in green biomass, $g/m^2/day$) and change in biomass with time is basic to understanding plant - herbivore dynamics (Noy-Meir 1975, Caughley 1976, Caughley and Lawson 1981, Caughley 1982, Krebs 1985, Begon and Mortimer 1986). The effect of grazing on forage determines proper herbivore stocking rate for any range as well as carrying capacity levels for natural ecosystems (Caughley 1976, 1977, 1981). In addition to herbivory, plant productivity is affected by plant physiology, weather patterns and site factors (Harper 1977, Begon and Mortimer 1986).

Plants make up for low levels of defoliation, and in some cases even overcompensate so productivity of grazed pastures may be greater than ungrazed pastures (McNaughton 1979, Cargill and Jefferies 1984, Belsky 1986, 1987; Paige and Witham 1987a, 1987b). Witham et al. (1991) discuss negative and positive effects of defoliation. They propose that plant responses to herbivory follow a continuum, from negative on one extreme to positive on the other. The effect of defoliation depends on such factors as apical dominance, growing conditions and, for plant communities, species composition.

Herbivory may benefit plants by removing litter, facilitating cross pollination of plants and altering successional trends. However, most studies have not considered the effect of herbivory on direct measures of fitness (such as the number of seeds per inflorescence, number of propagules per plant, percent germination success, percent seedling survival).

Negative impacts of herbivory on plants can be both direct or indirect. The negative effects on the fitness of the plant (McNaughton 1979, Paige and Witham 1987a, 1987b) include complete loss of seed production, reduced competitive ability, reduced resistance to intense defoliation, increased extinction of species at intense defoliation, abnormal plant structure, delayed sexual maturity, altered sexual expression and reduced commensal interactions with other plant taxa.

In general, overcompensation is expected when grazing occurs early in the growing season, when there is abundant (optimum) water, nutrients and light. Other factors favoring compensation are low intra - and inter-specific competition and faster plant growth. Plants undercompensate when grazing occurs late in the growing season and also in conditions of low (or limiting) water, nutrients, light and high competition.

Ultimately, resilience of a plant community to grazing depends on species composition, productivity and resistance to defoliation. Grazing removes dominance of a single species (through defoliation effect of thinning) hence encouraging competition. In the end, only species adapted to constant defoliation and have suitable modes of reproduction (specifically vegetative reproduction) will survive.

In this study, I considered the effects of defoliation on forage productivity at different intensities and frequencies, at different plant phenological stages and plant community changes in ungrazed pasture. The research hypotheses were:

- plants will over-compensate for defoliated tissues,
- compensation depends on plant biomass (or a proxy such as height),
- grazed pastures differ in species number and evenness from ungrazed pastures.

METHODS

Study area

This study was conducted at the Ministik Wildlife Research Station, Alberta, Canada. The area is characterized by low hills with scattered lakes and ponds. Plant growth begins in late April and ends in October. Permanent snow cover is established in November. The major vegetation types are *Populus* forest, *Bromus - Poa* grassland and *Carex* wetland. The grasses are dominated by brome grass *(Bromus pumpellianus*) and Kentucky bluegrass (*Poa pratensis*). Dicotyledonous plants include dandelion (*Taraxacum officinale*), clovers (*Trifolium* spp.), yarrow (*Achillea millefolium*), Aster (*Aster* spp.), Canadian thistle *(Cirsium arvense*) and wild strawberry (*Fragaria virginianus*).

Exclosures were established to determine the effects of intensity and phenological stage of defoliation on plant growth compensation. Also, permanent exclosures examined to evaluate the long-term (10 years) effects of grazing on plant community composition.

Effect of defoliation intensity

Forage height was taken as an index biomass. To calibrate the index, 30 samples were taken from a 30 cm by 30 cm quadrat. Forage of differing height and density were measured and clipped to the ground using garden shears. The samples were oven - dried at 60 C for about five days and weighed. A linear regression equation for biomass and height was:

Biomass, $g/m^2 = 77.92 + 6.06$ Height ($F_{(1, 28)} = 8.43$, $P = 0.019$, $R^2 = 0.58$).

Four heights (which required different intensities of defoliation to keep biomass about constant) were chosen: 2.5 cm (about 90 g/m^2), 7.5 cm (about 120 g/m^2), 15 cm (about 170 g/m^2), and 25 cm (about 230 g/m^2).

In a single pasture, eight plots of dimensions 1.5 meters by 1.5 meters were established. Each height treatment was randomly assigned to two plots and the available forage clipped to bring the plot to the appropriate height. Forage was clipped at least three times a week to maintain the height in each plot. All plots were clipped (using garden clippers) at each time, and the forage removed labeled, dated and oven - dried at 60 C for at least five days. Dry weight was then recorded. At the end of this experiment, forage samples from each plot were clipped to the ground, oven - dried and weighed to establish the biomass maintained in the plot. This was done between the middle of May and end of July 1994. Daily means from replicate plot treatment for a sampling day were used in analysis.

Defoliation in relation to plant phenology

Eight plots (each 4 by 4 meters) were used in this experiment. Two plots were assigned randomly to each stage of development (phenology) of the plant. The first two plots were defoliated in spring (May), the second pair was defoliated in June, and the last two pairs in late June 1994. The first pair of forage height was 3.5 cm and comprised early spring growth. The other pairs were established

as growing season progressed. The second pair (non - seeding) was defoliated at 13 cm, the third pair (inflorescence beginning to form) was defoliated at 18 cm, and the last pair (seeding) was defoliated at 28 cm. A control plot (2 by 2 meters) was paired with each "treatment" pair plot and left undefoliated but biomass was determined at the end of the experiment.

Before defoliation, samples (clipped in a 30 by 30 cm quadrat and oven dried at 60 C) were taken from each plot (including controls) to determine biomass at the time of defoliation. Each plot was mowed to 5 cm using a garden lawn mower. Plots were allowed one month (30 days) to grow before random samples (in a 30 by 30 cm quadrat) were clipped to the ground. Samples were then oven - dried at 60 C and weighed.

Composition and diversity in grazed and ungrazed pasture

The effect of grazing on plant community structure and composition was evaluated in two 40 by 40 meter exclosures which had been protected for over 10 years. Near each of these protected plots, a paired 30 by 30 meter exclosure was established. Each pair of exclosures (one protected and one continuously grazed) was about 0.5 km from each other, but in the same study location.

Five line transects were marked across each exclosure at five regular intervals, with the first and last transects being at least 5 meters from the edge of the exclosure. A 30 cm by 30 cm quadrat was used to sample along each transect in each exclosure. The position of each quadrat on the transect was determined randomly (from random number generator) until five sampling points for each transect were done. Plant species were identified and recorded, and the percent cover of each species estimated. Further, estimates of the proportion of bare ground and the measurement of height of (the majority) of plants in the quadrat were recorded. Each quadrat (along transects in protected and grazed plots) was used as a sampling unit and its estimates used in analysis.

Statistical analysis

Species richness and evenness is combined into a single species diversity index called "heterogeneity" (Simpson 1949, Good 1953, Hurlbert 1971). This incorporates number of species, abundance of individuals in each species,

species dominance and rareness. Both Simpson's Index of Diversity and Inverse of Simpson's Diversity were used to analyze plant community structure in grazed and protected pastures (Simpson 1949, Krebs 1989). Inverse of Simpson's Index of Diversity was used for easy interpretation as the number of equally common species required to generate the observed heterogeneity of sample (Peet 1974).

Mean values were compared using one - way analysis of variance (ANOVA). Multiple comparisons (after a significant one - way ANOVA) of the means to identify those which differed were done by Tukey's multiple comparison method. Comparisons of the effects of two "treatments" was done using independent or paired t - test (Zar 1984). All calculations and non - linear curve fitting was done with SYSTAT® software (Wilkinson 1990).

RESULTS

Effect of clipping height on biomass productivity

Productivity was highest when defoliation intensity was moderate (light) and declined when defoliation was either too heavy (as in plots maintained at low biomass) or too light due to competition and crowding of forage. The parabolic relationship of productivity (g) with (total i.e. green + dry) biomass (V) was (Fig. 3.1):

$$g = -6.09 + 0.10\ V - 0.0003\ V^2,\ R^2 = 0.50$$

Cumulative and daily production rates are summarized in Table 3.1. Average daily productivity differed among the intensities of defoliation ($F = 134.707$, $df = 3, 36$; $P < 0.001$, one - way ANOVA). Comparisons of mean productivity (Tukey's method) showed that pasture of light defoliation intensity (maintained at 15 cm) had higher productivity than pasture under high defoliation intensity (maintained at 2.5 cm, $P < 0.001$; and 7.5 cm, $P < 0.001$) and at low defoliation intensity (maintained at 25 cm, $P < 0.001$). Further, productivity of pasture defoliated at low intensity (25 cm height) was higher than pasture under high defoliation intensity (maintained at 2.5 cm, $P = 0.042$; and 7.5 cm, $P = 0.042$). Total productivity (cumulative) removed through defoliation differed among defoliation intensity treatments ($F = 10.216$, $df = 3,36$; $P < 0.001$, one -

way ANOVA). Pasture defoliated lightly achieved a higher total productivity than pasture under high defoliation (maintained at 2.5 cm and 7.5 cm) and low defoliation (maintained at 25 cm; $P < 0.001$ in both cases).

Effect of defoliation in relation to plant phenology

The effect of defoliation at different stages of plant development is summarized in Table 3.2. Defoliation at emergence and early vegetative growth increased productivity but the pattern was reversed once inflorescences appeared.

Composition and diversity in grazed and ungrazed pasture

Plant composition, height, abundance (cover), species number and ground cover showed a difference in grazed and long - term protected (ungrazed) pasture (Table 3.3). Grazed pasture had more plant species than protected (ungrazed) pasture ($T = 9.437$, $df = 98$, $P < 0.001$; Independent t - test in this section), and a shorter forage height ($T = -21.457$, $df = 98$, $P< 0.001$) than protected (ungrazed) pasture. Species dominance was greater in protected (ungrazed) pasture while species number and evenness were higher in grazed pasture.

Protected plots were colonized by aspen suckers but this was absent where pasture had been exposed to grazing. Therefore grazing is important in maintaining pasture, and in preventing succession to woody plants in boreal mixedwood ecosystem. *Bromus* excluded shade intolerant plants, hence increasing the proportion of bare ground in ungrazed pasture. Grazed pasture had less (or none) bare ground than protected (ungrazed) pasture ($T = -18.252$, $df = 98$, $P < 0.001$).

Simpson's diversity index was higher in grazed pasture (0.77 ± 0.01) than in protected (ungrazed) pasture (0.76 ± 0.02), but the difference was negligible ($T = -0.421$, $df = 98$, $P = 0.675$). The inverse of Simpson's index was greater in protected (ungrazed) pasture (4.83 ± 0.24) than in ungrazed pasture (4.58 ± 0.14), but the difference was minor ($T = 0.883$, $df = 98$, $P = 0.675$). This means that the probability that any two equally common species taken at random belong to the same species is higher (probability (Simpson's index) = 0.77)) in grazed

than in ungrazed (probability = 0.76) pasture; or that about 4.6 plant species (Inverse of Simpson's index) in grazed and 4.8 plant species in ungrazed pasture are needed to generate observed plant diversity respectively.

Protected plots were dominated by *Bromus* (36% in the protected pasture compared with 11.4 % in the grazed pasture). This grass species grows faster, is erect and tall hence has an advantage in interspecific competition for dominance of pasture where grazing is withdrawn. In grazed pasture, more evenness (Fig. 3.2) is evident and dandelion, white clover and yarrow are prominent.

DISCUSSION

Compensation depended on defoliation intensity and plant phenology. Forage defoliated to a height of 2.5 cm had a lower productivity because of high intensity of defoliation. Plants had not developed enough leaves and surface area to manufacture carbohydrates for both growth, tiller production and maintenance. Under light grazing conditions, plant tissues (leaves and stems) got sufficient time to regenerate and grow. Plants manufactured carbohydrates and mobilized these to translocate them to defoliated sites (McNaughton 1979). They possibly increased photosynthetic activity which was used to replace tissues removed through defoliation.

After winter when air and soil temperatures rise, growth is rapid and some products of photosynthesis are used for tissue growth. However this changes as plants mature as products of photosynthesis are directed to producing seeds or fruits (Harper 1977, Krebs 1985, Begon and Mortimer 1986). Compensation may be possible during active growth but not when growth is replaced by production of propagules. There seemed to be a critical level of defoliation intensity (and frequency), and stage of plant maturity beyond which compensation is not possible. This point seems to be between active plant growth and just before the onset of formation of inflorescence.

Compensation presumably occurs by stimulation of tillering following loss of apical meristem (Murphy and Briske 1992). Plant hormones produced in the apical meristem and young leaves, directly inhibit auxiliary bud growth. This

hypothesis (dating to the 1930's) has been abandoned because of inconsistencies, and the involvement of other plant hormones (particularly cytokinin) in apical dominance. The "cytokinin deficiency" hypothesis is the current hormonally - based interpretation of apical dominance. In this hypothesis, IAA produced in the apical meristem blocks the synthesis or utilization of cytokinin within auxiliary buds, hence inhibiting their growth. Cytokinin stimulates growth of auxiliary buds. Despite wide acceptance of the "cytokinin deficiency" hypothesis, many inconsistencies suggest that it is an incomplete interpretation of the physiological mechanisms.

Grazing - resistant genotypes of perennials propagate asexually as the inflorescence is often removed during defoliation (Stoy 1965). Grasses are known for interplant variation in somatic chromosome number. This makes vegetative reproduction capable of supporting evolutionary processes. Genetic modification is achieved through somatic sectoring in perenating organs (Nielson 1968). Evidence for somatic inheritance of tillering rate in asexually propagated clones has been reported (Breese et al. 1965). Herbivory effects may be both short-term (e.g. modifications of primary productivity) or long-term (e.g. changes in plant community structure and composition, and genetic properties).

An alternative interpretation of tiller initiation and regulation must integrate the hormone - based perspective with the effects of habitat factors. Defoliation in early plant phenology is likely to lead to compensation (Witham et al. 1991) but this interacts with intensity of defoliation. Light defoliation favors compensation over heavy defoliation. Variation in nutrient availability produces a gradient of plant compensatory responses. Of particular importance are nitrogen, carbohydrates and minerals, but these depend on plant physiology and limiting nutrients. Since plants need water for growth, maintenance and metabolism, sufficient (optimum) water favors compensation. Low light levels can stress plants, and light grazing exposes many tillers to light and thus stimulate growth. In ungulates, stimulatory effects of saliva on this process has been suggested (McNaughton 1979, Witham et al. 1991).

Species richness is greater in grazed plots because dominance is moderated through grazing activity (Sinclair and Norton-Griffiths 1979). Species

that can tolerate grazing (by depending on underground storage organs) form a horizontal leaf mat other than growing erect or being stemmy can dominate pastures. Grazing halts succession process and therefore keeps the pasture more nutritious than in protected plots.

These findings have implications for herbivore-plant equilibrium models (Noy-Meir 1975, Caughley 1976, Caughley and Lawson 1981, Caughley 1982, Spalinger and Hobbs 1992, Shipley and Spalinger 1992). These models seem to incorporate this compensation by considering absolute growth rate of forage. Productivity depends on intensity of defoliation and grazing pressure. Under light grazing conditions, and at allowable herbivore densities and resident period, defoliation may stimulate productivity.

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Table 3.1. Defoliation intensity for plots of varying biomass (and height). Forage was defoliated during growing season (from May to July). Mean±SE (n= 10)

Height maintained by repeated clipping (cm)	Biomass maintained in plots (g/m^2)	Cumulative green productivity removed through defoliation ($g/m^2/day$)	Green biomass productivity ($g/m^2/day$)
2.5 cm	$91.59 \pm 0.90^{a,1}$	4.50 ± 0.78	0.84 ± 0.05^{a}
7.5 cm	119.06 ± 1.44^{b}	3.34 ± 0.62	0.67 ± 0.11^{a}
15 cm	173.33 ± 1.04^{c}	14.31 ± 2.74	2.92 ± 0.14^{b}
25 cm	226.90 ± 0.63^{d}	6.28 ± 1.06	$1.19 \pm 0.07^{a,b}$

[1] Total forage removed to maintain specified pasture height

[a] Daily forage removal to maintain specified pasture height.

[a] Values with the same letter across the same variable do not differ at alpha of 0.05, but those with different letters differ.

Table 3.2. The effect of defoliation at different phenological stages on biomass and forage productivity (mean±SE, n=10).

Plot description	Biomass at defoliation (g/m^2)	Plant biomass 30 days after defoliation (g/m^2)		Productivity of defoliated and undefoliated plots (g/m^2/day)	
		Defoliated plot	Control plot	Defoliated plot	Control plot
Emergence (clipped at 3.5 cm)	102.5 ± 7.6[1, a]	187.8 ± 11.9[a]	111.0 ± 8.2	6.3 ± 0.4[a]	3.7 ± 0.3
Vegetative (clipped at 13 cm).	150.0 ± 6.5[b]	143.4 ± 4.9[b]	77.6 ± 1.8	4.8 ± 0.2[b]	2.6 ± 0.1
Inflorescence (clipped at 18 cm).	184.0± 1.4[c]	104.0 ± 3.5[c]	156.2 ± 1.8	3.5 ± 0.1[c]	5.2 ± 0.1
Seed set (clipped when 30 cm).	212.5 ± 4.0[d]	61.7± 2.4[d]	228.0 ± 1.2	2.1± 0.1[d]	7.6 ± 0.0

[a] Values of treatment and control (along rows) with the same letter do not differ at alpha of 0.05 (paired t-test). Compensation is demonstrated in earlier phenological stages (plots 1 and 2) and not when forage enter seeding stages (plot 3 and 4)

Table 3.3. Plant community structure in grazed and protected (ungrazed) pasture: plant composition, abundance (cover) and diversity (mean±SE, n=50).

Plant	Grazed species abundance (% cover)	Protected species abundance (% cover)
Aster (*Aster spp*)	0.0	4.9 ± 1.8
Kentucky blue grass (*Poa pratensis*)	8.4 ± 0.8 [1]	8.9 ± 5.2
Bromus (*Bromus pumpellianus*)	11.4 ± 1.6	36.0 ± 2.3
Dandelion (*Taraxacum officinale*)	24.2 ± 1.0	13.0 ± 1.9
Lathyrus (*Lathyrus spp.*)	3.4 ± 0.7	0.7 ± 0.3
Pink clover (*Trifolium spp.*)	2.3 ± 1.0	0.3 ± 0.3
Thistle (*Cirsium arvense*)	1.9 ± 0.9	9.7 ± 1.6
Timothy (*Phleum pratense*)	4.6 ± 1.0	0.4 ± 0.3
White clover (*Trifolium spp.*)	23.1 ± 1.2	0.3 ± 0.2
Yarrow (*Achillea millefolium*)	21.0 ± 1.3	0.2 ± 0.1
Average forage height (cm)	28.5 ± 0.7 [a]	57.7 ± 1.2 [b]
Non-green (bare) ground cover	0.2 ± 0.1 [a]	25.9 ± 1.4 [b]
Simpson's Index	0.77 ± 0.01 [a]	0.76 ± 0.02 [a]
Inverse of Simpson's Index	4.58 ± 0.14 [a]	4.83 ± 0.24 [a]
Total number of species	5.8 ± 0.2 [a]	3.2 ± 0.1 [b]

[1] Values compares grazed and protected (ungrazed) plots. Same letters indicate that values do not differ at alpha of 0.05, but those with different letters differ.

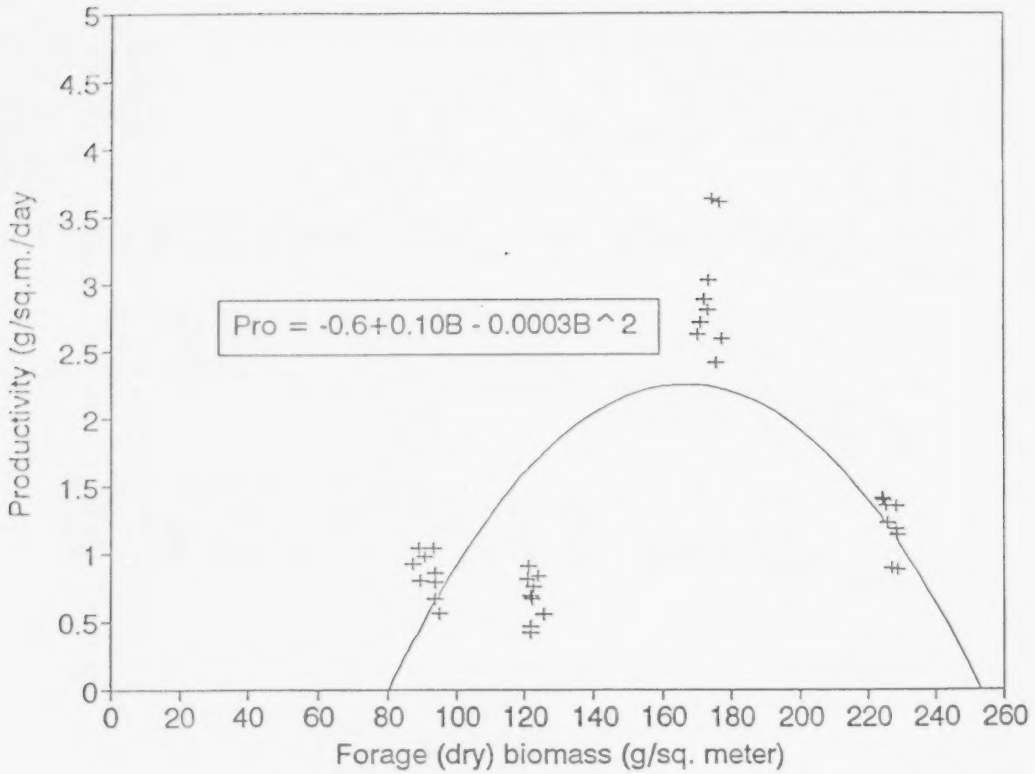

Fig. 3.1. The trend in productivity for pasture plots clipped and maintained at different constant forage biomass. The shape is parabolic, consistent with the logistic model. However, the fact that productivity is negligible until a critical biomass is reached is important in creating plant - herbivore stability.

CHAPTER 4
FORAGING RATES AND MECHANISMS

INTRODUCTION

The functional response of herbivores feeding on plants is crucial to understanding grazing system dynamics (Caughley 1979, 1981; Sinclair 1981, McNab 1985). A functional response describes the change in intake rate (of herbivores, predators and parasites and parasitoids) with increasing forage (plants, animal prey or hosts. As forage (prey density) increases, the rate of consumption by herbivores (predators) increases asymptotically (Holling 1959).

For most grazers, the asymptotic nature of the functional response is determined by handling time (time spent pursuing, subduing and consuming each prey item, and then preparing for further search). Another factor is searching efficiency which is determined by attack rate. This efficiency changes with predator age, prey size and hunger level (determined by length of time since last meal, as this determines attack rate and interest in food). Young inexperienced hunters spend more time searching for prey, hence have low efficiency compared to older experienced ones (Begon and Mortimer 1986). Larger prey need more "handling" (and possibly shorter "searching") time than small ones.

There are 3 types of functional response (Fig. 4.1). "Type 2 functional response" (asymptotic pattern discussed above) is most common for predator-prey, parasitoid - host, and herbivore - plant interactions. In the less common "type 1 functional response", intake rate is proportional to "prey" density until "saturation" (beginning of a plateau) is reached. At the saturation point, food intake is at the maximum, limited by only handling time. This "type 1 functional response" is an extreme form of "type 2 functional response" in which the handling time exerts it's effect suddenly, and not gradually as in "type 2 functional response" (Krebs 1985, Begon and Mortimer 1986).

The "Type 3 functional response" is S - shaped or sigmoid and occurs where attack rate increases or handling time declines with increasing prey

density (Begon and Mortimer 1986). It occurs when there is a change in handling time or attack rate (as in the case of a predator switching to an alternative prey). Though this is also rare, it can occur. An example is when an increase in prey density elicits an increased attack rate, whereas low densities elicit no interest from predators. At a higher prey density, attack rate (as well as handling time) is relatively constant .

Intake rates of herbivores are usually estimated from (i) pasture biomass depletion (Forbes and Hodgson 1985), (ii) direct estimation using esophageal or rumen fistulae (Laca et al. 1994a), (iii) bite rates, cropping rate, and grazing times, and (iv) fecal output, by total collection or inert markers (Jiang and Hudson 1992). The bite-count method which involves direct observation of bite rates, bite sizes and grazing times has been applied widely to wild ruminants because it involves the least manipulation or disturbance of animals (Wickstrom et al. 1984, Hudson and Nietfeld 1985, Renecker and Hudson 1986, Spalinger et al. 1988, Jiang and Hudson 1993).

Forage quality (nutrient content) is an important factor affecting intake rate (Willms 1978, Koerth and Struth 1991). Palatability is a plant characteristic that stimulates a selective response by herbivores (Heady 1964) and may determine cropping rates. Other factors that determine intake rates are plant canopy architecture as well as temporal and spatial variation of forage (Provenza and Balph 1990).

Heterogeneity of swards (as in height and composition) is a major determinant of selectivity of a patch and intake rate (Illius 1986). Maximum intake rates are achieved where both selection and heterogeneity occur in swards. However, intake rate in homogeneous swards is often higher than where there is heterogeneity (without selection) due to averaging in the latter case (Demment and Laca 1993). Bite size and bite dimensions are determined by canopy structure at and near the bite (Laca et al. 1992, Ungar et al. 1992, Laca et al. 1994b), and they change as patches are depleted. Such sward structure is defined by height, biomass density, and heterogeneity in composition.

Feeding rates depend on both plant morphological structure and herbivore anatomy (Spalinger et al. 1988). This rate is determined by bite size rather than directly by forage biomass or density (Renecker and Hudson 1986, Hudson and

Frank 1987, Spalinger et al. 1988, Ungar et al. 1991, Shipley and Spalinger 1992, Jiang and Hudson 1993). Intake rate does not respond to biomass as in predator-prey relationships (Holling 1959, 1965) because herbivores can chew forage while "searching" for the next bite. Thus "handling" food overlaps with "searching" for their next bite. Where forage is abundant, available or concentrated, intake rate dynamic is determined by the mechanics of manipulating, cropping and processing of food (Spalinger and Hobbs 1992).

The mouth of a herbivore serves two competing processes: cropping (selecting and apprehending a bite of plant tissues) and chewing (mastication, lubrication, and swallowing). The asymptotic intake relationship between intake rate and bite size results from competition between these two processes. Small bites require frequent interruptions of chewing, and thus reduce intake rates (Spalinger and Hobbs 1992). The processing rate is the amount of food chewed and swallowed (per minute). This rate sets the upper limit for intake rate, and the bite size influences the efficiency of forage processing.

This asymptotic relationship is represented by the Shipley and Spalinger (1992) models:

$$I = B * S$$

$$I = R_{max} S / (R_{max} h + S)$$

$$B = R_{max} / (R_{max} h + S) \text{ (Michaelis-Menton form).}$$

I is instantaneous intake rate (g /min), R_{max} is theoretical maximum intake rate of the herbivore, h is the mean handling time (usually min/bite), S is bite size (g / bite), and B (bites / min) is the cropping rate. As plant fiber and other structures that hinder mastication and ease of cropping increase, R_{max} declines, h increases, and intake rate declines even when bite size remains constant. R_{max} and h are estimated by a non-linear regression of the original data.

Caughley and Sinclair (1994) promulgate an alternative model of the functional response: $I = c (1 - \text{Exp} (- b V)$, where I is intake rate, c is maximum daily intake rate, b is the slope of the curve or a measure of grazing efficiency, and V is "prey" density. An inverse of the slope of this functional response estimates the forage biomass at 63% of satiation.

To determine how these models apply to a mixed feeder, I studied

foraging activity of wapiti (*Cervus elaphus nelsoni*) foraging on *Poa / Bromus* pasture and on cut sods. The hypotheses tested were:

- grazing modifies sward structure decreasing within - patch intake rates.
- plant structure (height, density, biomass) affects cropping rate and bite size, and hence instantaneous intake rate
- bite size increases with forage height and fiber content, while cropping rate declines due to handling constraints
- Instantaneous intake rate is affected by quality and phenology of forage.

METHODS

Study area and animals

This study was conducted between April and October at the Ministik Wildlife Research Station, Alberta, Canada in the summer of 1994. The major vegetation types are *Populus* forest, *Bromus-Poa* grassland and *Carex* wetland. The grasses are dominated by brome grass (*Poa pratensis*). Dicotyledonous plants include dandelion (*Taraxacum officinale*), clovers (*Trifolium spp.*), *yarrow (Achillea millefolium*), Aster (*Aster spp.*), Canadian thistle (*Cirsium arvense*) and wild strawberry (*Fragaria virginianus*).

Rocky Mountain wapiti (*Cervus elaphus nelsoni*) were used in the experiments. These animals were born at the station and were firmly habituated to human presence.

Research approach

In the field (pasture), daily consumption rates and factors affecting this rate were investigated. Of particular importance was the effect of forage depression and stocking rate on the dynamics of forage removal. However, pasture work would not provide detailed analysis of the factors and mechanisms affecting intake rate. Therefore, a controlled study was designed in which forage structural characteristics and quality were manipulated using cut sods. The strategy was based on the thesis that forage and cropping interactions at the bite level affect grazing dynamics at the patch level and paddock level (Murray 1991, Struth 1991, Demment and Laca 1993).

Pasture forage consumption rate and depletion

Cone - shaped movable cages were used to determine biomass changes and daily consumption rates. Four cages (1.5 meters in diameter and 1 meter high) were located randomly (using a random number generator for an x -, y - axis grid) in each of five pastures used on a rotational basis.

After locating a point and installing the movable cage in a pasture (before wapiti were allowed in) , two samples of forage in a 30 cm by 30 cm quadrat plot were clipped to the ground (using garden clippers) outside the cage. This gave (initial) biomass density before grazing. After 3 days (or less depending on pasture size and forage depletion rate), biomass density outside the cage and inside the cage were obtained by clipping. The cage was then relocated to another point randomly and the procedure repeated. This was repeated in all pastures throughout the growing season (May to August). Forage samples were labeled, dated and oven - dried at 60 C for about five days

Each pasture was studied in two consecutive sampling periods. The difference between the biomass inside the cage and the initial biomass was an estimate of forage productivity. This productivity data allowed calculation of stocking density (wapiti per unit area of pasture), stocking rate (wapiti per unit area of pasture per unit grazing time), and grazing pressure (wapiti per unit of plant production). A movable cage was the sampling unit and measurements around each movable cage was considered independent from other cages and other sampling days.

Effect of sward characteristics on intake rate

This study involved hand - constructed swards (HCS). These were 0.6 by 0.4 meter sods either cut fresh from the field (n=70) or obtained from a commercial sod distributor (n=12). Swards were trimmed and structured to provide a range of structure, density, height and biomass. They were chosen to fall in four broad categories: senescing swards, swards dominated by forbs, lush green swards, and sods from a lawn sod dealer. Each sod was considered the sampling unit and its measurements independent from other sods used in that sampling day or any other.

Three adult females wapiti (without calves) were fasted overnight in

individual pens in preparation for feeding experiments the next morning. The animals were free - ranging but were accustomed to people and the experimental protocol. Before each experiment, sods were gathered and weighed (with the supporting plastic tray). Another equivalent sward was placed nearby to account for moisture loss during the trial.

Between 8:00 AM and 12:00 noon each day, the experimental sward was offered to an individual wapiti and a video camera with an on-screen timer used to record the animal identity, date and time, duration of foraging, and number of bites. Swards were belted to a wooden platform to keep them firm when a wapiti was cropping. When the animal interrupted feeding, the sward and its control were re-weighed. A sample of forage from each sward was taken, labeled and weighed while still fresh, then oven - dried at 60 C for at least five days.

Cropping rate (bites / min) was calculated by dividing the total number of bites by the foraging duration. Bite size (g / bite) was calculated by dividing the weight consumed (after correcting for moisture loss using control) by the total number of bites. Intake rate (g/min.) was calculated by taking the product of bite size and cropping rate, or by dividing the total weight of forage consumed by the foraging duration. Proportion of moisture in the forage was determined by taking the difference between fresh and dry sample weight, dividing it by fresh weight.

To compare with pasture trials, daily intake rates (g/m^2) were calculated from instantaneous intake rates (g/min.) assuming an average grazing time of 7 hours each day (Gates and Hudson 1983, Hudson and Nietfeld 1985). By multiplying the grazing duration by instantaneous intake rates, daily intake rates were estimated.

Each sward was sampled for protein and neutral detergent fiber analysis. Protein was analyzed using an FP-428 Automatic Nitrogen Determinator® (1992 Leco Corporation). Neutral detergent fiber (NDF, an estimate of forage fibrousness) and dry matter content were determined using standard methods (Agriculture handbook #379, US Department of Agriculture).

Data analysis

Simple correlations were done with Pearson method, whereas multiple comparisons tests following a significant one - way ANOVA were done by

Tukey's method. To find the contribution of independent variables (e.g. forage height, density, moisture content and fiber content) to the variation of each dependent variable (intake rate, bite size, cropping rate, forage (protein) quality), multiple stepwise linear regression was used. Independent t - test was used to compare means of any two unpaired groups (Zar 1984). Non - linear model fitting and iterations, and other computations were completed with SYSTAT® software (Wilkinson 1990).

RESULTS

Pasture forage consumption rate and depletion

Average forage productivity (under grazing) was 63.4 ± 6.4 kg/ha/day. At a stocking density of 13.5 ± 0.4 head/ha, the average daily removal rate of pasture forage by wapiti was 7.0 ± 0.6 kg/head/day. Two consecutive sampling sessions are compared in Table 4.1. Total daily forage consumption, daily intake rate for each wapiti and forage productivity did not differ significantly between periods. Biomass at the beginning of grazing differed between consecutive grazing session (paired t-test; T = -3.539, df = 27, P = 0.001), and so did stocking pressure (T = 2.270, df = 27, P = 0.031), an index of consumption pressure for every unit of forage production.

Dry matter daily forage removal by each animal was associated with high biomass at the beginning of grazing (r = 0.267, P = 0.028, n = 68; Pearson simple linear correlations). Forage productivity was inversely related to grazing pressure (r = -0.578, P , 0.001, n = 68).

Intake rate on hand - constructed swards

Artificial swards were selected to provide a wide range of biomass, height, moisture, and neutral detergent fiber content (Table 4.2).

Intake rates differed significantly among sward types (F = 13.185, df = 3,78; P < 0.001, one way ANOVA). Intake rate of swards dominated by forbs was 35.5 ±2.0 g/min, followed by lush green swards (32.3 ± 1.4 g/min), then lawn (commercial) swards (24.4 ±1.7 g/min) and lastly fall senescing swards (21.5 ± 1.3 g/min). Mean comparisons (using Tukey's method) showed that swards

dominated by forbs had higher intake rate than fall senescing swards ($P < 0.001$) and lawn swards ($P = 0.006$), but not lush green swards ($P = 0.656$). Lush green swards had higher intake rate than fall senescing swards ($P < 0.001$) and lawn swards ($P = 0.012$). Lawn swards and fall senescing swards did not differ in intake rate ($P = 0.72$).

Bite size of fall senescing swards was 1.34 ± 0.04 g/bite, followed by lush green swards (1.18 ± 0.03 g/bite), then swards dominated by forbs (0.92 ± 0.04 g/bite) and lastly lawn (commercial) swards (0.59 ± 0.03 g/bite). Differences in bite size among sward types occurred ($F = 63.49$, $df = 3,78$; $P < 0.001$). Mean comparisons showed that fall senescing swards had a larger bite size than lawn (commercial) swards ($P < 0.001$), swards dominated by forbs ($P < 0.001$), and lush green swards ($P = 0.002$). Lush green swards had larger bite size than lawn (commercial) swards ($P < 0.001$), and swards dominated by forbs ($P < 0.001$). Swards dominated by forbs had a larger bite size than lawn swards ($P < 0.001$).

Cropping rate on lawn (commercial) swards was 41.1 ± 1.6 bites/min., followed by swards dominated by forbs (39.06 ± 2.59 bites/min.), then lush green swards (27.7 ± 1.2 bites/min.) and lastly fall senescing swards (15.9 ± 0.7 bites/min.). Differences in average cropping rates among sward types occurred ($F = 48.942$, $df = 3,78$; $P < 0.001$). Mean comparisons showed that lawn (commercial) swards had a higher cropping rate than fall senescing swards ($P < 0.001$) and lush green swards ($P < 0.001$), but not swards dominated by forbs ($P = 0.891$). Swards dominated by forbs had a higher cropping rate than fall senescing swards ($P < 0.001$) and lush green swards ($P < 0.001$). Lush green swards had a higher cropping rate than fall senescing swards ($P < 0.001$).

Higher intake rates were associated with high cropping rates (Pearson simple correlation, $r = 0.620$, $P < 0.001$, $n = 82$), and high protein content (Pearson simple correlation, $r = 0.438$, $P < 0.001$, $n = 82$). Low intake rates were associated with high neutral detergent fiber (NDF) (Pearson simple correlation $r = -0.446$, $P < 0.001$, $n = 82$) and forage height (Pearson simple correlation, $r = -423$, $P < 0.001$). However, only bite size (stepwise multiple linear regression, $r^2 = 0.535$, $P < 0.001$) and cropping rate (stepwise multiple linear regression, $r^2 = 0.384$, $P < 0.001$) explained most variation in intake rates among sward types ($F = 451.023$, $df = 2,79$; $P < 0.001$, one way ANOVA).

Larger bite size was associated with tall forage height (Pearson simple correlation, $r = 0.572$, $P < 0.001$, $n = 82$), and high NDF (Pearson simple correlation, $r = 0.244$, $P < 0.027$, $n = 82$). Small bite size was associated with high moisture content (Pearson simple correlation $r = -0.626$, $P < 0.001$, $n = 82$). However, forage biomass ($r^2 = 0.456$, $P < 0.001$, stepwise multiple linear regression) and forage height ($r^2 = 0.153$, $P < 0.001$) explained most variation in bite size among sward types ($F = 61.59$, $df = 2,79$; $P < 0.001$, one way ANOVA).

Higher cropping rate was associated with high protein content ($r = 0.356$, $P = 0.001$, $n = 82$). However, low cropping rate was associated with large bite sizes ($r = -0.695$, $P < 0.001$, $n = 82$), forage height ($r = -0.729$, $P < 0.001$, $n = 82$) and NDF ($r = -0.422$, $P < 0.001$, $n = 82$). Only forage height ($r^2 = 0.531$, $P < 0.001$, stepwise multiple linear regression) and forage biomass ($r^2 = 0.61$, $P < 0.001$) explained most variation in cropping rate among sward types ($F = 41.59$, $df = 2,79$; $P < 0.001$, one way ANOVA).

Functional response from hand constructed swards

Caughley and Sinclair 's (1994) model accounted for more variation (Fig. 4.2) than Shipley and Spalinger's (1992) model. In the Caughley and Sinclair (1994) form:

$$\text{Intake rate} = 29.78\,(1 - \text{Exp}(-3.63\ \text{Bite size})),\ R^2 = 0.55.$$

where C is maximum daily intake rate was 29.78 g/min and grazing efficiency (-3.63) is the slope of the relationship.

Using Shipley and Spalinger 's(1992) models and non - linear iterations, R_{max} was estimated to be 59.93 g/min and handling time to be 0.018 min./bite ($R^2 = 0.44$). Relating intake rate and bite size, R_{max} was estimated to be 53.35 g/min and a handling time to be 0.018 min/bite (Fig. 4.3):

$$\text{Intake rate} = 53.35\ \text{Bite size} / (0.96 + \text{Bite size}),\ R^2 = 0.48$$

Intake rate (Fig. 4.2b) was less strongly influenced by forage biomass but generally had the form of a "type 2 functional response"

Although intake rate had a describable relationship with bite size, it was not related to biomass (Fig. 4.4). However, biomass had a positive linear association with bite size and a negative linear relationship with cropping rate.

Comparison of pasture (field) intake and instantaneous intake rates

To convert instantaneous intake rates (g/min) into daily intakes, assumptions that the conditions of the experiments (e.g. forage characteristics and availability) were assumed constant for an entire foraging day. Average dry matter intake rate across sward types was 7.46 ± 0.24 kg/day (range: 3.70 - 12.46 kg/day, n = 82). Swards dominated by forbs had higher daily intake rate (9.19 ± 0.52 kg/day), followed by lush green pastures (8.38 ± 0.37 kg/day), then lawn (commercial) swards (6.32 ± 0.45 kg/day), and lastly fall senescent swards (5.57 ± 0.35 kg/day). These values bracket the empirically estimated intakes of wapiti on pasture (7.02 ± 0.56 kg/head/day).

DISCUSSION

Daily intake rate of wapiti on pasture was close to the 6 kg/head/day reported by Hudson and Watkins (1985). Daily intake rates in pasture varied because pasture conditions varied widely in biomass. The small daily intake estimate difference with that reported by Hudson and Watkins (1985) may be a reflection of losses through trampling. Higher estimates for sward experiments may be due to a "hunger" factor or experimental conditions.

Daily intake rates of wapiti on pasture were maintained even when average pasture biomass was declining. The likely explanation is that wapiti will move to patches of higher than average biomass to maintain intake rates (Jiang and Hudson 1993). Free ranging wapiti exercise patch choice (Jiang and Hudson 1993, Wilmshurst et al. 1995). Pasture "depression" is common where there is systematic foraging of randomly occurring (discrete) forage (Astrom et al. 1990).

Forage production for grazed pasture is both a function of available biomass and grazing pressure. When stocking density and rate increase, plants are cropped before leaves form and frequent reduction of plant tissues prevented photosynthesis and hence productivity. Moderate defoliation reduces competition, releases forage from apical dominance, allows more solar energy to reach buds and hence stimulates productivity (Frank and McNaughton 1992). Daily intake rates may show great variation because there is more heterogeneity and selection in the field (feeding station level) than at the bite level.

High intake rates for lush green swards and swards dominated by forbs were due to a larger bite size for lush green swards and a high cropping rate for swards dominated by forbs. Lush green and forb swards had low (NDF) fiber content but high protein content (hence better forage quality) and moisture. Such swards are more palatable to wapiti and therefore will respond with high intake and cropping rates. Senescing swards had a lower intake rate despite the large bite size because of poor quality (high fiber content and low protein content). Poor forage quality will have low intake rate (and cropping rate) even if bite size remains large.

The large bite size or cropping rate alone cannot compensate for factors that reduce intake rate. A small bite size in short commercial sods was associated with a low intake rate despite high cropping rate and high quality. Bite size in these swards was reduced by shortness of forage and possibly high moisture content. Small bites require frequent interruptions of chewing process so as to crop forage, and increased cropping rate to compensate for small bite size to keep intake rate at optimum. Further, short dense forage may also increase biokinetic costs of foraging due to the angle of the neck the herbivore uses to gather forage (Jiang and Hudson 1992). On the other hand, bite size did not increase intake rate in senescent swards. The competing processes of cropping and chewing (processing) set limits on intake rate. Large bite size for senescing fall swards increased handling time and hence slowed cropping rate.

While bite size and cropping rate differences among sward types was mainly a function of plant characteristics (quality (protein), moisture, height, biomass and fiber), intake rate was determined mainly by the interplay of cropping rate and bite size. There is also an important element of forage quality that seems to also affect both intake and cropping rates.

Long swards are sparse and easy for wapiti to crop. Easy cropping, access to leafy larger portions of plant and high fiber will result in a large bite size and possibly intake rate (if cropping is also optimal). However, there is an optimum bite size and cropping rate that maximizes intake rate. Higher bite size will eventually slow cropping and increase handling time, hence reducing intake rate. Cropping rate on the other hand is limited by morphology of mouth and tongue cropping apparatus. Fiber content and height affect intake rates by

influencing bite size and controlling handling time. But forage quality possibly operates independent of bite size, yet influences intake rates through cropping rate. This could be the reason why cropping rates were associated with high protein content, but not bite size.

Herbivores increase cropping rate in high quality forage. Lush green swards and swards with forbs were of high quality, and hence higher cropping rates. This may indirectly give information on how selection for high quality forage in a patch may affect intake. Intake will increase where selection and forage heterogeneity is high. This situation occurs when herbivores forage selectively for high quality forage. Therefore functional response of herbivores in the field (patch level) may be affected more by selective foraging and heterogeneity of swards rather than by the interactive influence of bite size, cropping rate and forage quality.

Functional response of herbivores is ultimately controlled by forage handling time. Forage with low quality, high fiber and low moisture requires more time in cropping and chewing. A relatively poor fit for all functional response models was possibly because of strong differences in forage characteristics. Nevertheless, the model may be more realistic despite the fit because forage in pasture is likely to be heterogeneous in composition, height, fiber content, protein content and level of maturity.

Other factors likely to affect intake rates are insects and parasites. Where hunting and other animal harassment are frequent, intake rate is reduced during these activities as wapiti have to remain vigilant. In winter, intake rate is influenced more by forage shortage resulting from snow barrier, and discomfort created by winter conditions. This is the subject of the next Chapter.

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Table 4.1. Pastures and variations of stocking density, forage consumed, productivity and biomass changes with grazing (mean±SE, n=4).

Pasture codes and Julian day	Stocking density (wapiti/ha)	Daily forage removal (kg/head/day)	Biomass before grazing session (kg/ha)	Forage productivity (kg/ha /day)
ME 10[1], 138	11	4.5 ± 1.1	1879 ± 72	109.2 ± 25.4
ME 11, 145	10	11.9 ± 2.4	1914 ± 197	48.6 ± 19.3
ME 20, 150	15	11.9 ± 1.4	1754± 384	4.1 ± 2.6
ME 21, 157	17	2.9 ± 0.8	1029 ± 101	113.7 ± 14.4
FR 10, 160	11	8.6 ± 1.9	1680± 331	32.4 ± 6.0
FR 11, 167	11	5.1 ± 0.7	1078 ± 70	39.7 ± 8.4
BI 10, 171	16	8.3 ± 2.5	2083 ± 179	52.8 ± 14.3
BI 11, 174	16	3.3 ± 2.3	1688 ± 380	90.0 ± 43.0
ME 10, 178	11	7.5 ± 1.3	2245 ± 143	41.4 ± 15.0
ME 11, 181	11	8.6 ± 3.8	2100 ± 91	57.7 ± 30.5
ME 12, 185	11	3.9 ± 0.9	1813± 468	160.3 ± 31.9
ME 20, 187	14	9.7 ± 1.8	2197 ± 73	61.1 ± 20.4
ME 21, 192	14	2.1 ± 0.7	1666 ± 318	11.1 ± 2.3
FR 10, 195	8	6.9 ± 3.4	2022± 162	79.2 ± 35.5
FR 11, 199	8	0.9 ± 0.1	1568 ± 87	56.1 ± 17.6
ME 20, 223	16	10.6 ± 1.8	217 ± 8	4.9± 1.3
ME 30, 226	30	4.6 ± 1.9	2051± 59	36.9 ± 6.6

[1] ME, FR and BI represent the 3 major location. Pastures with codes ending with 0 indicate the first grazing session, 1 indicates the second grazing session and 2 indicates the third grazing session consecutively on the same pasture. Pastures codes beginning with '1' indicate first pasture, '2' indicate second pasture while '3' indicate third pasture. There was a significant difference (alpha = 0.05) between consecutive grazing sessions even though biomass remained the same.

Table 4.2. Intake rate, bite size and cropping rate (mean±SE) of wapiti on various forage swards of differing characteristics (density, height, moisture content, protein content and fiber).

	Senescing swards	Swards dominated by forbs	Lush swards	Commercial lawn swards
Intake rate (g/min)	21.5 ± 1.3[b] (21)	35.5 ± 2.0[a] (10)	32.3 ± 1.4[a] (39)	24.4 ± 1.7[b] (12)
Bite size (g/bite)	1.34 ± 0.04[a] (21)	0.92 ± 0.04[c] (10)	1.18 ± 0.03[b] (39)	0.59 ± 0.03[d] (12)
Cropping rate (bites/min)	15.9 ± 0.7[d] (21)	39.1 ± 2.6[a] (10)	27.7 ± 1.2[b] (39)	41.1 ± 1.6[a] (12)
Biomass (g/m^2)	199.6 ± 4.9[b] (21)	146.9 ± 3.5[c] (10)	244.1 ± 4.0[a] (39)	70.1 ± 3.9[d] (12)
Forage height (m)	0.73 ± 0.06 (21)	0.20 ± 0.00 (10)	0.33 ± 0.01 (39)	0.09 ± 0.00 (12)
Forage density (g green forage / cm^3)	21.2 ± 2.6[c] (21)	30.7 ± 2.4[b] (10)	41.3 ± 1.0[a] (39)	35.8 ± 2.0[a,b] (12)
Forage moisture (%)	50.7 ± 3.0[c] (21)	71.1 ± 0.5[b] (10)	85.0 ± 0.8[a] (21)	83.8 ± 0.4[a, b] (12)
Neutral detergent fiber (%)	65.7 ± 1.3[a] (21)	45.7 ± 0.2[d] (21)	55.0± 0.2[c] (39)	61.6 ± 0. 2[b] (12)
Protein content (%)	7.28 ± 0.92[c] (21)	11.00 ± 0.11[b] (10)	16.60 ± 0.63[a] (39)	14.17 ± 0.51[a, b] (12)

[a] Same letter for each variable means that sward categories are not different ($P > 0.05$). Where letters do not occur, it means that all the means are different ($P < 0.05$).

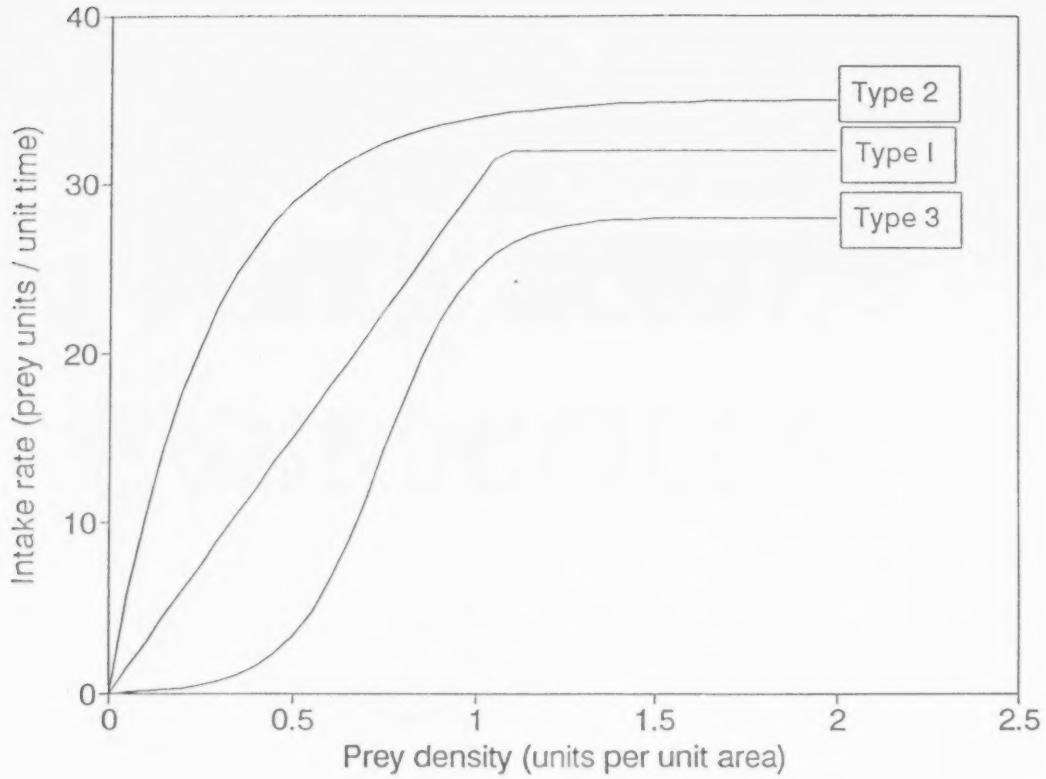

Fig. 4.1. Types of functional response. Type 1 functional response is when intake is proportion to intake until saturation occurs. In Type 2 response (most common), the rate of intake responds less and less as "prey" increases until saturation (asymptote) is reached. A Type 3 response (rare) occurs when their is a change in attack rate or handling time, as in when predators switch to alternative prey that is more abundant than the rare one (Holling 1965).

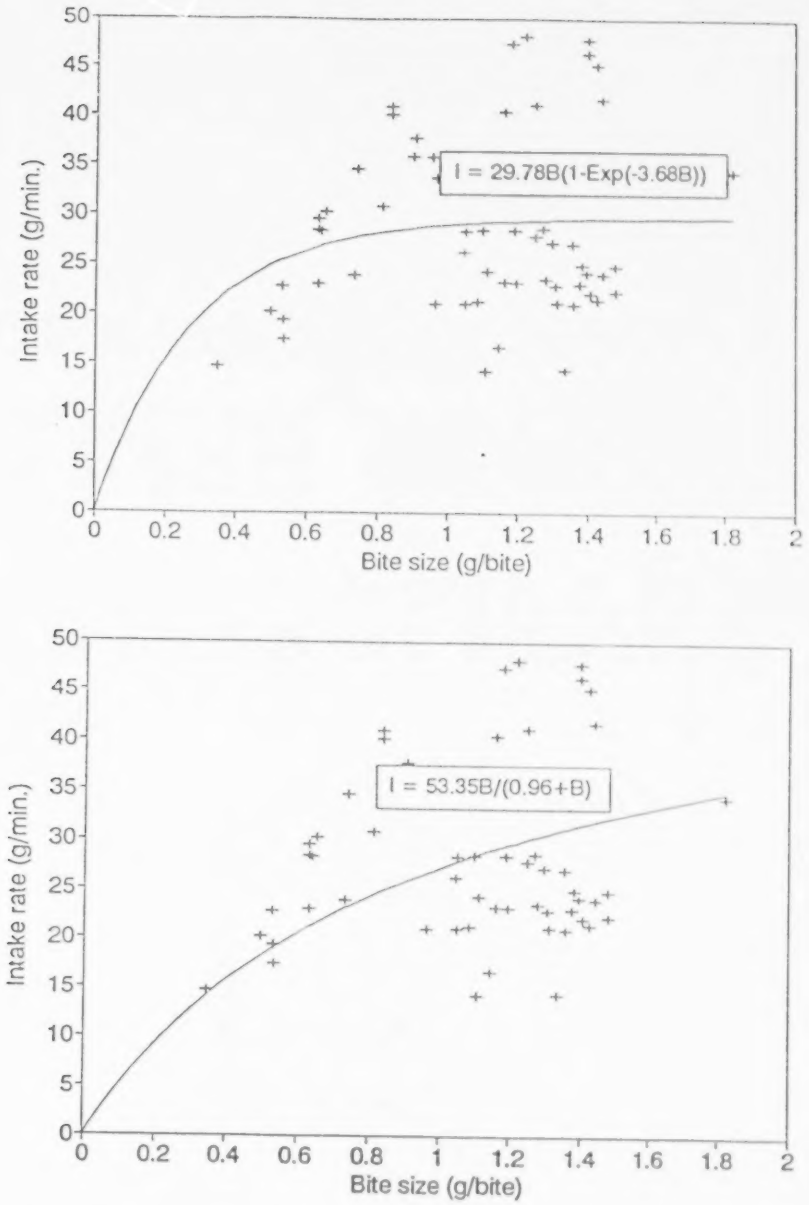

Fig. 4.2. Functional response of wapiti following models of Caughley and Sinclair (1994): I = 29.78 (1 - Exp(-3.63 Bite size), R^2 = 0.55 (top).; and Shipley and Spalinger (1992) model: I =53.35 Bite size / (0.96 + Bite size), R^2 = 0.48 (bottom).

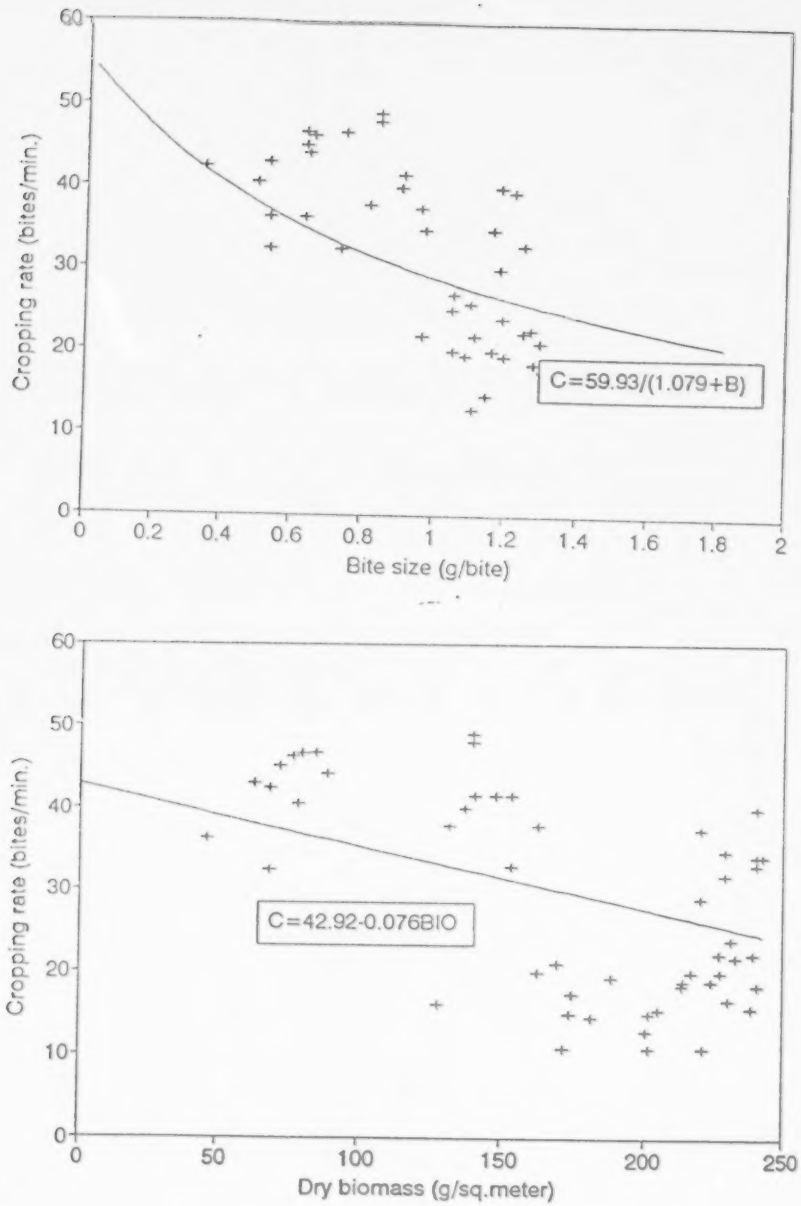

Fig. 4.3. Relationship between cropping rate and bite size (top), and between cropping rate and forage biomass (bottom): Cropping rate = 59.93 / 1.08 + Bite size, $R^2 = 0.44$, $P < 0.001$; Cropping rate = 42.92 - 0.076 Biomass, $R^2 = 0.20$, $P < 0.001$).

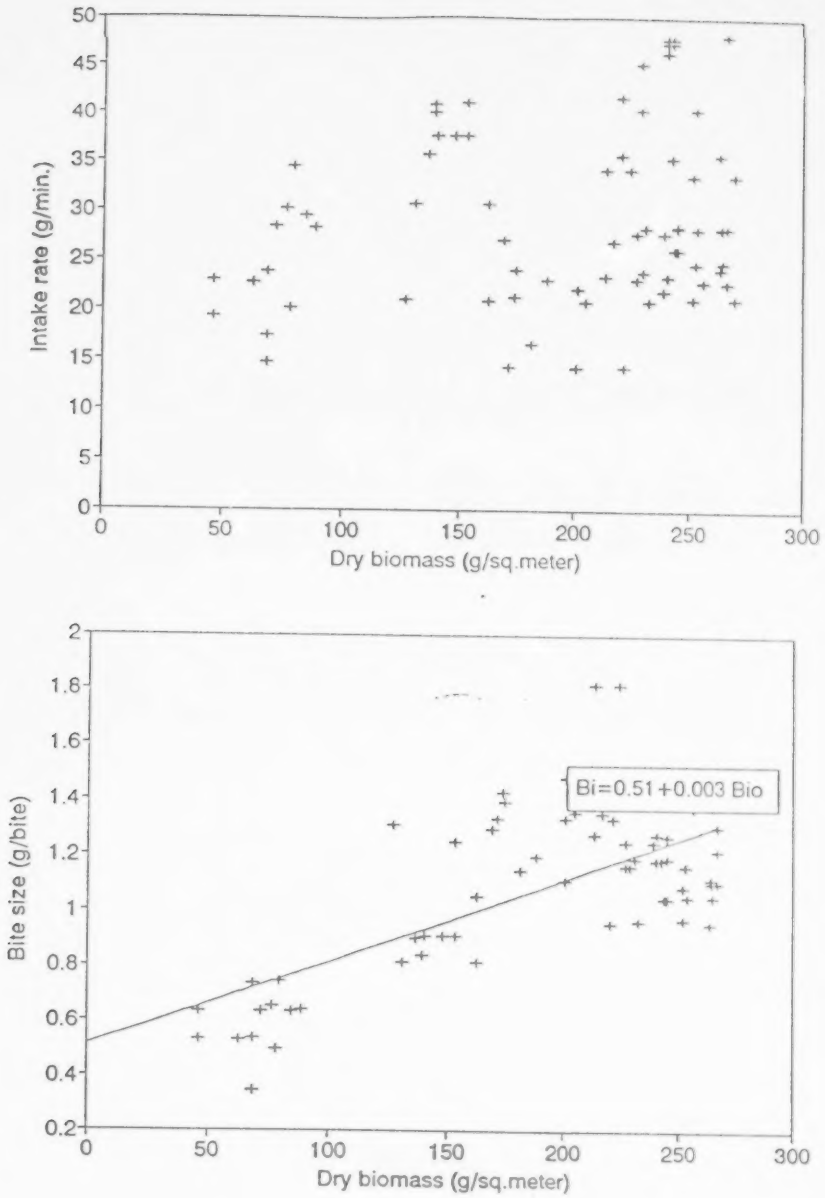

Fig. 4.4. Relationship between intake and forage biomass (top), and between bite size and biomass (bottom). There is no describable relationship between intake rate and biomass while it has a positive linear relationship with bite size (Bite size = 0.51 + 0.003 Biomass, R^2 = 0.46, $P < 0.001$). Functional response can therefore only be described in terms of bite size and cropping rate, not biomass.

CHAPTER 5
SNOW AND FORAGING EFFICIENCY

INTRODUCTION

The preceding chapter dealt with a grazing system during pasture growth (May to August). Winter offers great challenge to foraging due to lack of plant growth and limited forage availability due to covering by snow. The herbivore's functional response becomes not only a function of forage available, but also snow characteristics (e.g. depth and density).

Snow influences both energy intake and expenditures by restricting forage availability, increasing energy costs of foraging, altering habitat selection and movement patterns between foraging areas and increasing energy costs of locomotion (Parker et al. 1984, Hudson and White 1985, Fancy and White 1987, Dailey and Hobbs 1989). Sinking depth is determined by properties of snow cover and the characteristics of the herbivore. In light soft snow, the hoof penetrates to the ground and snow depth mainly influences energy costs of locomotion. Animal characteristics, such as brisket height and foot loading, affect locomotion (Kelsall and Telfer 1971). Dense snow or snow with a thin crust increases drag on the legs or body and walking causes the animal to lift its legs higher. These awkward movements interfere with efficient storage and recovery of elastic energy, resulting in a substantial increase in the cost of walking (Fancy and White 1987).

In snow density less than 0.10 - 0.20 g/cm^3 and depth of less than 25 cm - 50 cm, most northern ungulates can easily move and crater. But when density rises to 0.20 and 0.30 g/cm^3, snow provides inconsistent support and makes movement hazardous and digging difficult (Pruitt 1959, Kelsall and Prescott 1971). A further increase of density to 0.30 - 0.49 g/cm^3 provides more consistent support (Kelsall and Prescott 1971), but hinders cratering. Movement of wapiti, deer and caribou are limited with depths higher than 50 cm - 60 cm even at densities of 0.10 - 0.30 g/cm^3 (Telfer 1967, Henshaw 1968).

The overall objective of this study was to determine how snow and forage

characteristics interact to determine foraging rates of wapiti. The hypotheses were:

- snow limits winter feeding rates and proportion of forage consumed,
- biomass available at cratered sites determines forage consumed (reward).

If snow characteristics limit foraging, then I expected a correlation between snow variables and forage consumption. Likewise forage biomass consumed was expected to differ among sites and correlate with snow characteristics, whereas feeding rate was expected to differ with forage biomass weights, length and time of cratering activity, and correlate with certain snow variables.

METHODS

Study area and animals

The study was conducted at the Ministik Wildlife Research Station, Alberta, Canada. The area is characterized by low hills with scattered lakes and ponds. Spring growth begins in late April and ends in October. Permanent snow cover is established in November and persists until April. The major vegetation types are *Populus* forest, *Bromus-Poa* grassland and *Carex* wetland. The grasses are dominated by brome grass (*Bromus pumpellianus*) and Kentucky bluegrass (*Poa pratensis*). Dicotyledonous plants include dandelion (*Taraxacum officinale*), clovers (*Trifolium* spp.), *Achillea millefolium*, Aster *(Aster* spp.), Canadian thistle *(Cirsium arvense)* and wild strawberry *(Fragaria virginianus).*

The Rocky Mountain wapiti ecotype (*Cervus elaphus nelsoni*) was used in the investigations. Although only a few were hand reared, they were all born on the station and habituated to human presence. During the study, they received alfalfa and barley pellets to supplement pasture. However, most of their daily nutrient requirements were obtained from native vegetation.

Research approach

Snow characteristics in open and canopy closed habitats were investigated to find if canopy closure affected snow characteristics. Most winter

cratering by wapiti was within a forest and I wanted to see if snow characteristics changed with canopy. In 1994, I determined how snow characteristics differed in open (unforested) grass and forested areas and how these affected foraging site selection and the proportion of forage consumed. Once this was established, the proportion of forage consumed at any cratering site was determined to provide an index of foraging efficiency under the prevailing weather conditions. In the second winter, detailed information on foraging rates at each station (cratered site) also was collected to determine what snow characteristics best described intake.

Snow characteristics

Snow characteristics were measured near 20 feeding craters and adjacent control sites in open and forest habitats in February and March of each year. Open habitats had no trees or overhead canopy whereas forest habitats had trees and overhead canopy. The control sites were four compass points located one meter away from cratered sites. Snow depth and density were taken with a snow core sampler.

Forage reward at sites

Forage reward was determined at cratered and control sites between 26 February and 23 March 1994. Multiple use of a crater (previously exposed by another wapiti) was allowed until it was no longer in use before measurements were taken. At the four compass points, approximately one meter from the cratered site, forage under snow was collected in a similar manner. The forage comprised all fallen leaves, grasses and twigs that could serve as forage. Dry weight was determined after oven-drying at 60 C. Twenty sampling sites were examined.

Cratering and feeding behavior

Feeding rates were defined as the amount of forage consumed per unit time per unit area of forage. Wapiti were followed and observed when actively foraging between 15 February and 13 March 1995. After the wapiti had abandoned the crater, forage remaining was collected in a quadrat of 30 cm by 30 cm. The quadrat mostly fell within the area browsed at the bottom of a crater.

Time was recorded at the start of any cratering activity and at the end. Time was broken into two activities: cratering and foraging. At the same time, the number of leg strokes used to expose forage was recorded. Fifty-five sites were examined.

Statistics

The effect of treatment (canopy closure and Julian day) on snow characteristics, proportion of forage consumed (foraging efficiency) and forage intake rates were determined using two-way Analysis of variance (ANOVA). Simple correlations were done with Pearson method, while multiple comparisons tests following significant one - way ANOVA were done with Tukey's multiple comparison method. To find the contribution of an independent variable (snow characteristics) on a dependent variable (forage consumed, proportion of forage consumed and intake rate), multiple stepwise linear regression was used (Zar 1984). Computations were completed with SYSTAT® software (Wilkinson 1990).

Pearson correlation was used to determine the relationship between snow characteristics (depth, density, water equivalent weight and snow column weight) and foraging indices. Paired t - test was used to determine if snow characteristics differed between forested and open habitats in the study area (Zar 1984). Multivariate Analysis of Variance (MANOVA) was used to simultaneously assess the effects of habitat, Julian day, and the interactions between them on snow characteristics. This method was used to account for the multiple interdependence of snow characteristics (Baker and Baker 1984, Morrison 1976). All statistical analysis were done by *SYSTAT, Inc.* Software (Wilkinson 1990).

RESULTS

Snow characteristics in relation to habitat

Snow characteristics did not vary significantly by habitat (Tables 5.1, 5.2). However, Julian day and the interaction of habitat x Julian day affected some variables. Snow depth and water equivalent weight were affected by winter conditions prevailing on the Julian day as these variables easily change when it

snowed (snow depth: $F = 80.939$, $df = 1, 36$, $P < 0.001$; water equivalent weight : $F = 138.042$, $df = 1, 36$, $P < 0.001$).

Forage consumption and efficiency

Snow conditions and associated foraging parameters are summarized in Table 5.3. Snow density (0.26 ± 0.01 g/cm^3) and water equivalent weight (122.05 ± 2.32 g) had the lowest fluctuation among cratered sites. Snow depth (41.40 ± 1.33 cm), forage consumption efficiency (the ability of wapiti to forage a larger proportion of forage available; 0.49 ± 0.02) and forage biomass available (514 ± 21 g/m^2) had moderate fluctuation. The highest fluctuation among cratered sites occurred in forage consumed (253 ± 17 g / cm^2) because of a combined variation in snow hindrance and forage biomass.

Forage biomass consumed and forage consumption efficiency were affected by forage biomass available, snow depth, water equivalent weight and snow column weight (Table 5.4). Forage consumed depended on available forage ($r = 0.657$, $n = 80$, $P < 0.001$, simple regression). Forage consumed was inversely related to snow depth ($r = - 0.345$, $n = 80$, $P = 0.002$). Forage consumption efficiency (quotient of the weight of forage biomass consumed to the weight of forage biomass) also varied inversely with snow depth ($r = - 0.265$, $n = 80$, $P = 0.017$).

Variation in forage consumed among sites was best explained by forage biomass available at sites ($r^2 = 0.442$, $P < 0.001$, multiple stepwise linear regression), snow column weight ($r^2 = 0.087$, $P < 0.001$) and snow density ($r^2 = 0.004$, $P = 0.086$). Variations in forage biomass consumed were therefore largely explained by the forage biomass available and snow column weight.

Intake rate and feeding behavior

More detailed measures of intake rate and feeding behavior were added in 1995 (Tables 5.5, 5.6). Compared with the previous year, snow was shallow but dense. Although snow and forage characteristics varied little among sites, feeding rate (13.91 ± 1.09 g/m^2/min) and effort expended per unit feeding rate (3.11 ± 0.42 strokes of leg/g/m^2/min) fluctuated widely among cratered sites.

Feeding rate (g/m^2/min) was inversely associated with the effort (leg

strokes/g/m^2/min) to clear snow ($r = -0.569$, $n = 55$, $P < 0.001$). Feeding rate also increased with forage biomass ($r = 0.27$, $n = 55$, $P = 0.04$). This is also expected in situations where forage is limiting, but feeding rate is expected to level off at a certain biomass. Feeding rate, forage consumed and effort were least affected by snow (Table 5.6).

DISCUSSION

The differential effect of habitat canopy closure on snow characteristics varies from one location to another and from day to day. In this study, snow characteristics were not affected by canopy. This was possibly due to the small sizes of these habitats and the open nature of aspen/poplar stands. However, weather conditions, such as bursts of warm weather that lead to snow melting, whether it has been snowing or not, and strong wind movement, can increase or sweep away volumes of snow affecting both density and depth.

Trees can trap snow and shield it from movement, hence generally supporting high volumes and depth of snow. Snow density and depth change with wide fluctuations in weather conditions, such as snowing followed by warm weather that leads to melting. In terms of wapiti foraging activities, snow density (below 3.0 g/cm^3) was not a major hindrance as the range was generally below critical thresholds (Kelsall and Telfer 1971).

In the study area, snow characteristics did not hinder movement, but certainly (with a combination of forage biomass availability) affected winter foraging activities. This is expected because access to forage is determined by snow depth and density (Fuller 1966, Telfer and Kelsall 1971, Van Camp 1975, Houston 1982). These snow characteristics make foraging energy costly, and whether wapiti will continue foraging will depend on the discomfort level of prevailing weather conditions and forage biomass reward. Forage biomass consumed and forage consumption efficiency increases in conditions where snow cover is low and available forage biomass is abundant, but they decline in areas with dense, deep and heavy snow. The choices are made in accordance to rewards versus energy expenditure (Charnov 1976, Jiang and Hudson 1993).

Feeding rate is affected by available forage biomass, snow density and snow column weight. Feeding rate increases with forage biomass because

intake of forage is not limited by encounter or searching rates when forage is abundant. Feeding is expected to increase with abundant forage biomass until a saturation point is reached. Feeding rate declines with increasing snow density and depth because they limit access to forage and result in increased effort (and energy expenditure). When most of the foraging time is spent searching (removing snow barriers to foraging), there is less time to actually forage.

Results show that when more effort (time, energy, concentration) is spent exposing forage, feeding rate declines possibly because the whole foraging activity is dominated by the effort to expose forage. When more energy is spent and only minimal net gain from forage is obtained, the cumulative effects lead to poor body condition and worsen the ability of wapiti to forage as winter progresses. To avoid this, more ardent forage selection is necessary.

Feeding rates of wapiti in winter are affected by its efficiency (forage and site selection to reduce effort), forage biomass rewards and snow characteristics (mainly snow depth and snow density). Wapiti spend more time browsing on twigs and other browse above snow surface (Gates and Hudson 1983). This selective foraging may be an appropriate strategy for energy maximization.

From the standpoint of modeling the dynamics of plant-herbivore systems, snow ensures a non-grazable reserve which reduces the ability of herbivores to overshoot long-term equilibria. It also introduces a strongly stochastic element which may prevent approaching a stable equilibrium.

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Table 5.1. Snow characteristics in open and closed habitats

Snow characteristics	Forest[1] (n = 20)			Open (n = 20)		
	Mean[2] ± S.E	Min	Max	Mean ± S.E.	Min	Max
Snow density (g/cm^3)	0.26 ± 0.01	0.17	0.31	0.27± 0.01	0.170	0.33
Snow depth(cm)	43.41± 3.29	29.51	72.00	41.58 ± 3.17	25.50	70.00

The habitats were classified as open or forested. A habitat was considered open even if it lies within a forested habitat but the tree canopy did not cover it. It was considered forested when it fell within trees and covered by the canopy.

Snow characteristics did not differ (alpha = 0.05) between forested and open habitats.

Table 5.2. Effects of habitat and Julian day on snow characteristics, 1994

Effects	Snow characteristics	Univariate ANOVA (df = 1, 36)		Multivariate (MANOVA) Wilk's Lambda (df = 4, 33)	
		F	P	F	P
Habitat	Snow density (g/cm^3)	0.002	0.97	0.42	0.25
	Snow depth (cm)	0.041	0.84		
Julian day	Snow density (g/cm^3)	1.966	0.17	0.45	0.00
	Snow depth (cm)	138.0	0.00		
Habitat x Julian day interaction	Snow density (g/cm^3)	0.018	0.895	0.30	0.29
	Snow depth (cm)	0.01	0.904		

[1] The MANOVA test

Table 5.3. Snow and forage characteristics, 1994

Variables	Mean ± S.E (n=80)	Range		Coefficient of variation
		Min	Max	
Snow density (g/cm^3)	0.26 ± 0.01	0.19	0.35	0.17
Snow depth (cm)	41.40 ± 1.33	23.00	60.00	0.29
Forage consumption efficiency	0.49 ± 0.02	0.28	0.85	0.39
Forage biomass consumed (g/cm^2)	252.94 ± 16.68	35.22	789.76	0.59[1]
Available forage biomass (g/cm^2)	513.83 ± 21.29	115.78	932.96	0.32

Table 5.4. Effects of snow and forage characteristics on foraging parameters of wapiti, 1994.

Effects	Consumption (response)	Univariate NOVA test (df = 1, 74)		Multivariate (MANOVA) tests	
		F	P	F	P
Available forage biomass (g/m^2)	Forage consumption efficiency	0.23	0.57	231.07	<0.001
	Consumed forage biomass (g/m^2)	68.60	0.00		
Snow density (g/cm^3)	Forage consumption efficiency	2.84	0.10	1.44	0.24
	Consumed forage biomass (g/m^2)	2.74	0.10		
Snow depth (cm)	Forage consumption efficiency	15.62	0.00	7.70	<0.001
	Consumed forage biomass (g/m^2)	13.11	0.00		
Water equivalent weight (g)	Forage consumption efficiency	18.45	0.00	9.16	<0.001
	Consumed forage biomass (g/m^2)	14.31	0.00		

Table 5.5 Snow and forage characteristics and foraging parameters, 1995

Variables	Mean ± S.E	Range		Coefficient of variation
		Min	Max	
Snow density (g/cm^3)	0.20 ± 0.01	0.07	0.28	0.24
Snow column weight (g/cm^2)	3.70 ± 0.06	1.05	6.32	0.29
Snow depth (cm)	28.95 ± 0.31	16.65	37.50	0.24
Forage consumption efficiency	0.16 ± 0.01	0.01	0.47	0.53[1]
Forage biomass consumed (g/cm^2)	81.7 ± 3.1	2.6	320.0	0.62[1]
Forage biomass available (g/cm^2)	500 ± 12	117	733	0.41
Depth to forage (cm)	15.8 ± 0.3	2.0	29.5	0.32
Feeding rate (g/cm^2 /day)	13.9 ± 1.1	1.8	45.7	0.58[1]
Effort expended per unit of forage consumed (g/cm^2/day)	3.1 ± 0.4	0.5	22.2	1.00[1]

Table 5.6. The effect of snow characteristics and biomass on feeding rate, forage consumption efficiency and effort wapiti use to expose forage under snow, 1995.

Effects [1]	Consumption	Univariate NOVA test (df = 1, 49)		Multivariate test (Wilks' lambda df=3,47)	
		F	P	F	P
Available forage biomass ($g/m^{2)}$	Feeding rate (g/m^2/min.)	5.252	0.026	5.125	0.004
	Forage consumed ($g/m^{2)}$	14.667	0.000		
	Effort (strokes g/m^2/min.)	0.425	0.518		
Snow density (g/cm^3)	Feeding rate (g/m^2/min.)	2.154	0.149	1.152	0.338
	Forage consumed ($g/m^{2)}$	3.162	0.082		
	Effort (strokes g/m^2/min.)	1.653	0.205		
Snow depth (cm)	Feeding rate (g/m^2/min.)	0.046	0.831	1.616	0.198
	Forage consumed ($g/m^{2)}$	0.777	0.382		
	Effort (strokes g/m^2/min.)	1.161	0.287		
Water equivalent weight (g)	Feeding rate (g/m^2/min.)	0.062	0.804	3.449	0.024
	Forage consumed ($g/m^{2)}$	5.155	0.028		
	Effort (strokes g/m^2/min.)	0.012	0.914		

[1] Feeding rate was affected by available forage biomass and snow column weight. Forage consumed was affected by available forage biomass, snow column weight and water equivalent weight. Effort was affected by water equivalent weight only.

[2] Available forage biomass, water equivalent weight and snow column weight affected consumption responses. Even though Wilk's Lambda F statistic is reported, both Pillai Trace F statistic and Hotelling-Lawley has the same values.

CHAPTER 6
SYNTHESIS

The stability of grazing systems is of interest both to managers of wildlife conservation areas and of mixed species commercial ranches (Caughley 1977, Caughley and Sinclair 1994). The central question addressed by my thesis is whether and how stability can be achieved between forage and herbivore populations in an insularized conservation area. I conducted work on captive wapiti grazing volunteer pastures at the Ministik Wildlife Research Station and applied my results to Elk Island National Park as a case study.

I used Caughley's (1976, 1977) approach to modeling grazing systems. The first step of my research was to establish patterns of growth in a grazed plant community over the growing season. The second step was to map the functional response of wapiti both experimentally and on pasture under different stocking rates. This information was then combined and analyzed using "predator-prey" graphs (Noy-Meir 1975) to form a base on which further tests could be done with information on population dynamics. An interpretation of this work and discussion of its contribution and limitations are given below.

IMPORTANCE AND JUSTIFICATION OF STUDY

The stability of native grazing systems is becoming increasingly important as fragmentation and insularization increases through such human encroachments as settlement, farming and urbanization. In this regard, wildlife ecologists and managers are interested in whether grazing systems (plant - herbivore interactions) can achieve stability without intervention. Further, they want to know the equilibrium (if possible), its level for plants and herbivores, and where the turning and stable points lie on the plant biomass continuum. To study this problem, information on plant growth patterns (forage population dynamics), functional responses of herbivores (foraging dynamics), numerical responses (population dynamics) are needed (Caughley 1977).

The current consensus in many ecological and conservation circles is to allow conservation areas to remain natural and allow physical and biological ecosystem processes to proceed unfettered by human intervention. But some of these conservation areas have a history of active management, whereas others have been insularised to such an extend that it is not known whether such natural ecosystem processes can persist. While ecologists have argued for a possibility of a grazing system achieving stability unaided (e.g. Caughley 1976), a history of active management, fragmentation and insularisation leave modest hope.

Elk Island National Park in central Alberta is struggling with the question of whether herbivores can reach an equilibrium with their forage supply without active management. This question is significant given encirclement of the park by human settlement and a game fence which inhibits historical dispersal and migration pattern and disrupts normal predator-prey-plant relationships. This study attempted to give insight to this problem by addressing the overall question of whether the wapiti - forage grazing system of the Beaver Hills are inherently stable. This study was an important step in determining whether stability of a grazing system is probable in the aspen-boreal ecoregion and whether the current practice of range improvement through prescribed burning is likely to hasten an equilibrium between plants and animals.

ADVANCEMENT IN UNDERSTANDING OF GRAZING SYSTEMS

Grazing systems can stabilize, go extinct, lock into a stable limit cycle or fluctuate chaotically. Mechanisms and threshold that change a grazing system from stability to the alternative outcomes, and the interactions and life history strategies used to achieve stability are of great ecological interest. This knowledge can be directly applied in management decisions, especially the effects of artificial crowding and confining of wild herbivores.

My study appears to be the second (to a reindeer - lichen study by Gaare and Skogland 1980) that attempts to investigate the stability of a grazing system using a graphical model (Noy - Meir 1975). I attempted to isolate and identify mechanisms and population strategies that influence the outcome of plant-

herbivore interaction. This study offers room for further complimentary studies using an interactive model (e.g. Caughley 1976).

This study advanced our fundamental understanding of grazing system dynamics. My study suggested that both natural (e.g. rain) and artificial (e.g. fertilizer or range burning) factors that change life history strategies of plants (or herbivores) will affect the ease with which equilibrium can be achieved. Resilience of plants to grazing (and this may be an life history strategy adapted over interactive evolutionary time) may be the ultimate factor determining stability of a grazing system.

Many models and approaches in the fields of applied ecology have tackled the problem of carrying capacity and grazing system stability. My study adopted the graphical model of Noy-Meir (1975) and suggests further development through interactive modeling (Caughley 1976) using the numerical response data collated and analyzed by Blyth (1995). This study revealed the complex and confounding variables specific to herbivores and plants that determine grazing system stability.

The graphical approach applied in this study assumes set - stocked (i.e. managed) herbivore populations and probes how range condition will respond to graded stocking levels. This approach considers only plant growth patterns and the functional response of the herbivore population under predetermined stocking rates. Plant growth and consumption in relation to pasture biomass are graphed and stability points examined. Such an exercise does not give details of the nature of stability (such as whether it's a stable state or stable limit cycle).

The alternative interactive (simulation) approach is universal and can be applied to free-running as well as set-stocked systems. The method uses numerical response data in addition to the two basic relationships used in graphical methods. The nature of stability is evident and findings and effect of population parameters (and their variation) can further be tested through simulation studies. Because of its greater scope, my original plan was to apply this method using population parameters from a companion study on the herbivore guild at Elk Island National Park (Blyth 1995). However, the critical relationships proved difficult to derive because corresponding vegetation measures were not available.

LIMITATIONS OF THIS STUDY

Despite the promise of this approach to modeling plant-herbivore interactions, my study suffered from several methodological and interpretive limitations. Methodological limitations involved insufficient replications and consequent pseudo - replication. Interpretive difficulties involved inherent limitations in the graphical method as well as lack of a close fit of plant growth patterns to expected theoretical patterns.

The patterns of plant growth curves and functional response (foraging dynamics) did not closely follow theoretical patterns. Small differences in the shape of these curves would greatly influence the conclusions of this study. Further work should look at the sensitivity and confidence intervals of all the graphs in this study and determine whether conclusions still hold with shifts in these curves.

Sampling design constraints imposed by logistic concerns were the basic problem. Rigorous hypothesis testing requires that sampling units and replicates are clearly defined. For treatments (such as irrigation, manuring and defoliation), the sampling unit should be a plot and a minimum of thirty are needed. Using randomly sampled quadrats in a few (two plots for some treatments) is a form of pseudo-replication. The best approach (though overwhelming in data collection and handling) could have been more than thirty independent plots for each treatment rather than relying on quadrat samples (actually sub- samples are replicates).

However, where patterns and dynamics of variables (e.g. forage biomass and species diversity) over time and across seasons are of primary interest, repeated measures in at least two replicate plots will meet the objectives. When comparing species diversity, the ideal case is to have many (over thirty) plots which have been protected from grazing and a similar number which have continually been exposed to grazing for comparison. Where possible, such replicates are the sampling units instead of random quadrat sub - samples obtained from two replicate plots of grazed and protected treatments. However, I do not feel that the overall differences in diversity indices and studies was missed because of this limitation. Nevertheless, I recognize that pseudoreplication

occurred in this study and could compromise the validity of certain statistical tests and conclusions.

THE WAY FORWARD

There are three important ways forward. The first is to obtain other relevant plant and herbivore population parameters which together with those empirically derived in this study, may be used for an interactive model such as that of Caughley (1976). Blyth's (1995) time-series analysis of herbivore populations at Elk Island is an important step in this direction but Blyth's (1995) data did not specifically look at the population sizes with varying forage biomass nor the numerical response of herbivores to the dynamics of biomass abundance and availability.

The second challenge is dealing with seasonality. The role of winter browsing in plant and herbivore foraging dynamics is not clear, but seems a probable determinant of stability. Most models on grazing system apply to the tropics where plants grow throughout the year. Hence, the models use annual time-steps which may be inappropriate for strongly seasonal environments. Winter browsing probably affects plant productivity in the growing season, or possibly not dependent on the intensity of winter browsing. This demands further research.

The third challenge is to consider a grazing guild instead of a single herbivore species. To attempt to analyze and predict stability for multi-herbivore species will simulate a more natural grazing system. Of course the complexity of the challenge and the model used to resolve it multiplies geometrically. On the other hand, models of this sort are never intended to be used predictively. Their value lies in providing insight and stimulating critical thinking and research.

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